

TRANSMISSION OF UNIVALENT CHROMOSOMES
IN INTERSPECIFIC CROSSES OF
BRASSICA

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ABSTRACT

Transmission of the nine univalents from the c genome was studied in the F_1 progenies of six backcrosses of species with the aacc and aa genomes of Brassica.

The distribution of these univalents at first anaphase as measured by the chromosome number in the F_1 backcross populations approached that expected from random distribution. There were some deviations from random distribution but in all crosses the intermediate classes were represented by large numbers and the extreme classes by relatively few individuals. The mean number of univalents for the six backcross populations varied from 3.5 to 5.4. Only small differences in transmission through the male and female gametes were observed.

At first anaphase the distribution of univalents in F_1 (B. campestris x B. napus) and its reciprocal was 4.39 and 4.57 respectively, and 4.22 for the F_1 (B. napus x B. trilocularis). These means are in all cases close to the expected mean of 4.5.

The number of univalents in the F_1 plants from the backcrosses was negatively associated with pollen fertility. The frequency of monosomics, double monosomics and triple monosomics in progeny of F_1 crosses with B. napus was quite high (29.84%).

A gene conditioning the formation of erucic acid was transferred from B. campestris to B. napus.

TABLE OF CONTENTS

	<u>PAGE</u>
INTRODUCTION -----	1
LITERATURE REVIEW -----	4
MATERIALS AND METHODS -----	18
RESULTS -----	24
A. CYTOLOGICAL STUDIES -----	24
(a) Cytology of the Parents -----	24
(b) Cytology of F ₁ Hybrids -----	27
(c) Chromosome Transmission -----	33
(d) Pollen Fertility -----	51
B. CHEMICAL STUDIES -----	54
DISCUSSION AND CONCLUSIONS -----	57
SUMMARY -----	66
BIBLIOGRAPHY -----	68

LIST OF TABLES

<u>TABLE</u>		<u>PAGE</u>
I	Chromosome numbers in F ₁ (<u>B. napus</u> x <u>B. rapa</u>) x <u>B. napus</u> . -----	9
II	Transmission of extra chromosomes of triploids and other polyploids to their progeny. -----	12
III	Transmission of extra chromosomes of pentaploid <u>Triticum</u> hybrids to their progeny. -----	15
IV	Morphological description of the species employed as parents. -----	19
V	Fatty acid composition of seed oils from the species employed as parents. -----	20
VI	Frequency distribution of univalents at first anaphase in F ₁ hybrids from interspecific crosses in <u>Brassica</u> . -----	31
VII	Frequency distribution of lagging univalents at first anaphase and telophase in F ₁ hybrids from interspecific crosses in <u>Brassica</u> . -----	32
VIII	Frequency distribution of chromosome numbers in the backcross progeny of interspecific crosses in <u>Brassica</u> . -----	34
IX	Frequency distribution of chromosome numbers in the backcross progeny of interspecific crosses in <u>Brassica</u> . -----	45
X	The mean percentage pollen fertility in the backcross progeny of interspecific crosses in <u>Brassica</u> . -----	52
XI	The mean percentage pollen fertility in the backcross progeny of interspecific crosses in <u>Brassica</u> . -----	53
XII	Fatty acid composition of seed oils from the F ₁ progeny of the cross <u>B. napus</u> x F ₁ (<u>B. campestris</u> x <u>B. napus</u>). -----	55
XIII	Frequency distribution of univalents in the backcross progeny of interspecific crosses in <u>Brassica</u> . -----	61

LIST OF FIGURES

FIGURE

PAGE

- 1 Frequency distribution of chromosome numbers in
the backcross progeny of; a, B. napus x F₁
(B. campestris x B. napus); b, F₁ (B. cam-
pestris x B. napus) x B. napus; c, theo-
retical. ----- 36
- 2 Frequency distribution of chromosome numbers in
the backcross progeny of; a, B. napus x
F₁ (B. napus x B. trilocularis); b, theo-
retical. ----- 43
- 3 Frequency distribution of chromosome numbers in
the backcross progeny of; a, B. campestris x
F₁ (B. napus x B. campestris); b, F₁ (B. napus
x B. campestris) x B. campestris; c, theo-
retical. ----- 46
- 4 Frequency distribution of chromosome numbers in
the backcross progeny of; a, F₁ (B. napus x
B. trilocularis) x B. trilocularis; b, theo-
retical. ----- 48

LIST OF PLATES

<u>PLATE</u>		<u>PAGE</u>
I	Meiotic and somatic chromosomes of the parent species. -----	26
II	Univalent behaviour in the F ₁ (<u>B. campestris</u> x <u>B. napus</u>) and somatic complement of F ₁ (<u>B. napus</u> x <u>B. trilocularis</u>). -----	29
III	Typical somatic chromosome complements in the F ₁ of the cross or its reciprocal (<u>B. napus</u> x diploid) x <u>B. napus</u> . -----	38
IV	Typical pod characteristics of F ₁ plants from the cross <u>B. napus</u> x F ₁ (<u>B. campestris</u> x <u>B. napus</u>) illustrating the effect of aneuploidy on seed set. Chromosome numbers are shown below pods.-	40
V	Typical somatic chromosome complements observed in F ₁ of the cross or its reciprocal (<u>B. napus</u> x diploid species) x diploid species and aberrant chromosome complements. -----	50

INTRODUCTION

The genus Brassica comprises a large number of species some of which are an important source of edible oil. Of these, Brassica napus L. and Brassica campestris L. commonly known as summer rape and turnip rape respectively, are cultivated in Canada.

Rapeseed oil is primarily used as an edible oil but a small portion is used for industrial purposes. The major portion is utilised in the preparation of margarine and shortenings, etc. In the recent past, the utilization of this oil by Canadian processors has further increased its demand. According to Downey and Bolton (9) 250,000 acres are required under this crop to meet the domestic requirements for edible oil.

In view of the rapid development of acreage under rapeseed in Canada, which increased from 7,500 acres in 1951 to 699,800 acres in 1964 (3,9) improvement in the quality of rapeseed oil is necessary to make it more competitive with other vegetable oilseeds. Some undesirable effects of rapeseed oil have been attributed to the deficiency of saturated fatty acids and high erucic acid content (2).

Strains of B. napus with seed oils which are free of erucic acid have been isolated at the Plant Science Department of the University of Manitoba. Thus there is a good prospect of bringing the rapeseed oil up to the standards of other edible oils which are low in erucic acid (42). Inheritance studies in B. napus have revealed

that erucic acid is conditioned by two independent gene loci and that their dosage effect is additive (13,41).

For transfer of desirable traits such as the erucic acid free characteristic and self-compatibility from species to species, knowledge of the manner in which chromosomes are transmitted is essential for efficient transfer of traits. Moreover, in the last decade spectacular results have been achieved in the field of plant aneuploidy through the development of aneuploid series which provide a means of associating genes with different chromosomes. The aneuploid work in wheat by Sears (38), in barley by Tsuchiya (45), in maize by McClintock and Hill (18), in tobacco by Clausen and Cameron (5), in oats by McGinnis (19) are a few examples. This type of research work is becoming more and more fascinating to the various workers engaged in this field.

The studies of chromosome transmission in interspecific crosses of Brassica will be of special significance in providing preliminary but basic information regarding the production of aneuploids in Brassica. This work would also result in increasing the genetic variation due to different chromosomal combinations and thus would widen the prospects of breeding in this crop. The determination of fatty acid composition of the backcross populations would also shed some light on the genetics of erucic acid content of the rapeseed oil.

The research work reported here deals with the chromosome transmission in interspecific crosses of Brassica species with haploid chromosome numbers of 19 and 10 and the utilization of this information

on chromosome transmission in assessing the scope of aneuploidy
and the genetics of rape.

LITERATURE REVIEW

The origin of species has long intrigued research workers. The genus Brassica which is endowed by nature with a good deal of variation in chromosome number was considered an ideal material for unravelling the secrets of species formation. This resulted in the production of a formidable volume of literature. The papers selected for review deal with the rather limited number of reports more or less directly related to the transmission of chromosomes in Brassica and the more numerous papers dealing with the same topic in other species. The review is organised into sections dealing with cytological phenomena and chemical composition of the seed oil.

A. CYTOLOGICAL

It is well known that the chromosomes that are paired at meiosis have an equal opportunity of orientation to either pole. Considerable knowledge on the behaviour of haploids and polyploids has been gained from studies in the Triticinae. A review of the subject has been published by Riley and Chapman (36). A few facts known about univalents are:

(i) Univalents are distributed to the poles at random or the distribution to the two poles is numerically approximately the same.

(ii) Univalents may pass to either pole without dividing at first division of meiosis and may divide normally at second

division.

(iii) There is tendency for the univalents to lag at the first division. They may divide at the first division and then lag at the second. Usually the lagging chromosomes are not included in the nuclei resulting from meiosis but appear as micro-nuclei in the quartet of spores.

(iv) Univalents which pass to one pole without dividing probably divide at the second division.

(v) Occasionally the univalents may divide at first division of meiosis and again at second division.

(vi) In some cases most or all of the univalents have the tendency to pass to one pole.

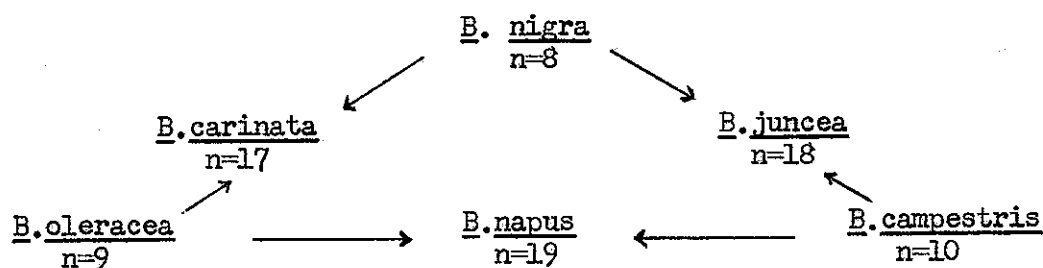
Olsson (29) studied the cytology of B. campestris var. oleifera Metzg. and observed ten bivalents at metaphase. Alam (1) and Sikka (39) studied the cytology of B. campestris L. ssp. trilocularis (Roxb.) Olsson. This species showed the formation of ten bivalents at diakinesis and metaphase. The entire meiotic behaviour was regular.

Nagai and Sasaoka (26) reported the chromosome number of B. napus L. as $2n=38$. All the chromosomes showed complete pairing and chiasmata terminalised fully. This number was confirmed in a number of varieties of B. napus (14,46).

Morinaga (23) was the first to suggest that high chromosome

species B. carinata Braun (n=17), B. juncea Coss (n=18) and B. napus L. (n=19) have been derived as amphidiploid hybrids between the species B. nigra Koch (n=8), B. oleracea L. (n=9) and B. campestris L. (n=10). He based his observations on the studies of chromosome pairing in species hybrids and determined the intergenomic relationships between different Brassica species. The genomic constitution in diploid Brassica species B. campestris, B. nigra, and B. oleracea was designated as aa, bb and cc respectively and those of amphidiploid species B. juncea (aabb), B. napus (aacc) and B. carinata (bbcc).

The relationship between these species can be illustrated by the famous triangle of U (46). He was the first to synthesize B. napus from crosses between B. campestris and B. oleracea followed by doubling of chromosomes. Later U's hypothesis was verified by synthesis of three polyploid species (10,11,30,33).



Morinaga (20) studied the meiotic behaviour of F_1 hybrids between B. napella (n=19) and the 10 chromosome species, B. pekinensis, B. rapa, B. chinensis and B. japonica. In each case the chromosome number in the somatic cells of the F_1 hybrid was 29

and meiotic metaphase showed ten bivalents and nine univalents. Morinaga (21), Sasaoka (37), U (46) and others studied F_1 hybrids between 10 chromosome species and the amphidiploid species, B. napus ($n=19$), and B. juncea ($n=18$). In the case of hybrids with B. napus they found ten bivalents and nine univalents and in the hybrid with B. juncea, ten bivalents and eight univalents. Both these amphidiploid species had one common genome aa which showed complete pairing with the aa genome furnished by B. campestris while univalents of the extra genome showed random assortment.

Olsson (30) analysed the chromosome numbers of hybrid plants between B. campestris ($n=10$) and B. nigra ($n=8$). Eighteen chromosomes were observed in 9 of the 11 plants studied while the other two plants showed the chromosome numbers of 28 and 36. The 28 chromosome plant was the result of an unreduced gamete from B. campestris and a normal gamete from B. nigra. The plant having 36 chromosomes was the result of unreduced gametes from both parents or the result of somatic doubling in the early stages of zygote development. The presence of unreduced gametes in Brassica has also been observed by a number of early workers (12,25).

Olsson (30) observed that seed setting was better when the parent with the higher chromosome number was employed as a female parent. Similar results have been reported in Brassica by several authors (15,21,27,40,43). Morinaga (21) also reported that when

the chromosome number of both species is the same the reciprocal crosses are successful.

Haploids in Brassica have been reported by several authors. Morinaga and Fukushima (24), Komatsu (16), Olsson and Hagberg (32) described their cytological behaviour in B. napus, Ramanujam (34) in B. campestris, Ramanujam and Srinivaschar (35) in B. juncea and Kuriyama and Watanabe (17) in B. carinata. However, very little is known about their progeny which could give some clue about the functional gametes produced by them. Olsson and Hagberg in the course of their study of haploid B. napus observed that mostly the gametes with $n=19$ were functional. Inflorescences that were prevented from cross-pollination set no seed but when abundant pollen from the normal diploid plant was supplied some seeds were formed. The seeds with the exception of a few plants with 57 chromosomes yielded normal diploid plants. Thus only female gametes with 19 or possibly 38 chromosomes were functional.

The behaviour of univalents in Brassica as understood from the species hybrids and haploids studied by several workers (17, 20, 21, 22, 23, 24, 32, 39) may be summarized as follows.

At metaphase the univalents were mostly scattered around the bivalents and at first anaphase the bivalents separated first and then the univalents. The univalents which happened to be present at the equator divided and disjoined to the poles and occasionally

both halves moved to the same pole. Univalents which were present away from the equator did not show any signs of splitting and migrated to the nearest pole. Some univalents were transferred to the poles without division, others divided at late anaphase and telophase, still others located on the periphery were not included in the spindles. Occasionally all the univalents were included in the daughter nuclei. Lagging chromosomes were also observed at second anaphase. A few univalents or their daughter halves might lag on the spindle. The division of univalents or their elimination resulted in the formation of gametes with a variety of chromosome numbers.

The transmission of univalents to the F_1 from crosses between species differing in chromosome number has been studied in several species but there appears to be only one report dealing with this subject in Brassica. Catcheside (4) determined the chromosome numbers in eight F_1 plants in the progeny of the cross, (B. napus x B. rapa) x B. napus. The data are given in the following table.

TABLE I. Chromosome numbers in F_1 (B. napus x B. rapa) x B. napus. (Catcheside (4)).

No. of chromosomes	30	31	32	33	34	35
No. of plants	1	0	4	2	0	1

From the data it is clear that the gametes with intermediate

numbers 13 and 14, were functional and that the frequencies of chromosome numbers observed could be due to random distribution of univalents.

Tokumasu (44) studied the behaviour of aneuploids in the progeny of tetraploid Raphanus sativus ($4x=36$). Besides eutetraploids the progeny consisted of hypo- and hyper-ploids of tetraploids and triploids. These aneuploids when selected as seed parents were responsible for the collapse of tetraploidy. The triploids, including hypo- and hyper-triploid individuals, were the most important for the breakdown of tetraploidy as they are the first to start diploidization. In the tetraploid population the diploid gametes will have the highest frequency followed by $2x \pm 1$, $2x \pm 2$, $2x \pm 3$ ---- $2x \pm n$ gametes. As a consequence the $4x$ individuals would be the maximum in number followed successively by $4x \pm 1$, $4x \pm 2$, $4x \pm 3$ ---- $4x \pm n$. Thus eutetraploids are maintaining eutetraploidy and at the same time aneuploidy. These hyper- and hypo-tetraploids keep reverting to eutetraploidy while some keep maintaining the aneuploidy. However, all these aneuploids have a strong tendency towards diploidization, from tetraploids to triploids and from triploids to diploids.

While there appears to be lack of information on the transmission of univalent chromosomes in crosses between species of Brassica, a good deal of work has been done concerning the problem in triploids or higher polyploids of plant species by backcrossing

with the parents. The results of these studies have been reproduced in Tables II and III (28).

The data in Table II indicates that marked differences in the functioning ability of male and female gametes from the F_1 hybrid sometimes occur. This difference is very evident in Oenothera and in most of the cases all the possible female gametes are functional and most male gametes with intermediate chromosome numbers are not functional. In Nicotinia, Pyrus and in one case in Oenothera when the transmission through the female is considered, there is greater frequency of intermediate types, while the majority of the species crosses show selective functioning ability for male and female gametes with the same or nearly the same chromosome number. In most of the cases there is great deviation in the observed frequencies of segregates from the theoretical frequencies. The only case of chromosome transmission studied in Brassica Catcheside (4) indicates transmission of intermediate chromosome numbers in frequencies approaching random distribution.

The results of chromosome transmission studies by different authors in Triticum pentaploid hybrids shown in Table III (28) indicate that apart from one instance where transmission of intermediate chromosome numbers is high all other cases consistently lack the transmission of intermediate numbers and favour extreme classes. Generally, a higher frequency of intermediate chromosome numbers tends to be transmitted through the female than through the male gametes.

TABLE II. Transmission of extra chromosomes of triploids and other polyploids to their progeny. (Nishiyama (28)).

Material	Cross	No. of extra univalents													Sum	Author
		0	1	2	3	4	5	6	7	8	9	10	11	12		
<u>Through eggs</u>																
<u>Oenothera lamarckiana</u> , x = 7	3x x 4x	1	2	12	21	25	19	6	1							87)
"	3x x 2x	1	9	4	2	2	0	1	1							20)
<u>O. biennis</u> ¹ , x=7	3x x 4x	2	7	7	3	6	5	1	1							32)
"	3x x 2x	41	26	4	0	0	0	0	0							71)
<u>O. semigigas</u> x <u>velutina</u> , x=7	"	3	35	19	13	3	4	4	0							81
<u>Datura stramonium</u> , x=12	"	24	33	10	0	0	0	0	0	0	0	0	0	0	0	67
<u>Solanum lycopersicum</u> , x=12	"	10	35	14	2	0	0	0	0	0	0	0	0	0	0	61
<u>Zea mays</u> , x=10	"	0	1	3	1	3	1	0	1	0	0	0				10
<u>Pyrus malus</u> , x=17	"	0	0	0	1	4	1	5	10	2	4	1	1	1	1	31
																Moffatt (1931)

12

¹Besides, one plant has 36 chromosomes (2n).

TABLE II CONTINUED

Material	Cross	No. of extra univalents													Sum	Author
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	
<u>Fragaria</u> , x=7	3x x 2x	9	11	2	1	0	0	1	0	(1)					25	Yarnell (1931b)
<u>Nicotinian tabacum</u> x=12	6x x 4x	0	0	2	1	3	2	8	1	4	5	3	1	0	30	East (1933)
<u>N. rustica</u> (4x) x <u>paniculata</u> (2x) x=12	3x x 2x	0	0	1	1	4	0	8	0	4	2	0	0	14 ²	34	Goodspeed, C. and C. (1926)
" x=12 ³	"	0	5	2	3	13	16	16	6	6	2	0	0	0	69	Lammerts (1929)
"	3x x 4x	0	0	0	0	4	0	7	0	0	0	0	0	0	11	Goodspeed, C. and C. (1926)
" ⁴	"	0	0	0	1	3	0	5	12	8	3	0	0	0	32	Lammerts (1931)
<u>Petunia</u> , x=7 ⁵	"	0	0	0	0	0	0	0	11	(2)					13	Dermen (1931)
<u>Avena barbata</u> (4x) x <u>strigosa</u> (2x) x=7	3x x 2x	1	0	0	0	0	0	0	0	0					1	Nishiyama (1932)

continued

²After Lammerts (1929) these plants might have ca.48 chromosomes (2n).³Besides, 14 plants have ca.48 chromosomes (2n).⁴Besides, 35 plants have ca.60 chromosomes (2n).⁵Besides, one plant has 36 chromosomes (2n).

TABLE II CONTINUED

Material	Cross	No. of extra univalents													Sum	Author	
		0	1	2	3	4	5	6	7	8	9	10	11	12			13
<u>Through pollens</u>																	
<u>Oenothera lamarckiana</u> x=7	4x x 3x	3	1	0	0	0	0	1	10	(3)					18)	Van Overeem (1921)	
"	2x x 3x	0	2	0	0	0	0	0	0)		
<u>O. biennis</u> x <u>lam.</u> , x=7	"	36	6	0	0	0	0	0	0)		
)		
<u>Solanum lycopersicum</u> , x=12	"	2	0	0	0	0	0	0	0	0	0	0	0	0	2	Lesley (1928)	
<u>Zea mays</u> , x=10	"	27	6	2	0	0	0	0	0	0	0	0	(1)		36	McClintock (1929)	
<u>Fragaria</u> , x=7	"	9	1	0	0	0	0	1	0						11	Yarnell (1931b)	
<u>Nicotinia rustica</u> (4x) x <u>paniculata</u> (2x), x=12	4x x 3x	0	0	0	0	0	0	4	3	2	2	0	3	29	(1)	44	Lammerts (1931)
<u>Petunia</u> , x=7	2x x 3x	39	12	0	0	0	0	0	0						51	Dermen (1931)	
<u>Avena barbata</u> (4x) x <u>strigosa</u> (2x) x=7	4x x 3x	0	0	0	0	0	0	0	0	1					1	Nishiyama (1932)	

() Unexpected plants.

These aberrant plants could be produced by mating between unreduced gametes and normal ones.

TABLE III. Transmission of extra chromosomes of pentaploid Triticum hybrids to their progeny. (Nishiyama, (28))

Crosses	No. of extra univalents									Total	Author
	0	1	2	3	4	5	6	7			
4x x F ₁	4	0	0	0	0	0	0	0		4	Kihara (1925)
"	7	1	0	2	3	1	2	1		17	Watkins (1927a)
"	32	11	3	2	4	2	0	2		56	Sax (1928)
"	33	19	6	6	4	2	3	10		83	Thompson and C.(1928)
"	21	12	2	2	3	0	1	0		41	Kihara,W. and Y.(1933)
Total	97	43	11	12	14	5	6	13		201	
6x x F ₁	0	0	1	0	1	2	3	3		10	Kihara (1925)
"	6	2	0	1	2	1	4	3		19	Watkins (1927a)
"	10	5	4	2	1	2	3	6		33	Thompson and C.(1928)
"	14	9	5	2	6	4	7	19		66	Kihara,W. and Y.(1933)
Total	30	16	10	5	10	9	17	31		128	
F ₁ x 4x	2	4	2	1	1	1	0	0		11	Watkins (1927a)
"	42	21	17	9	7	2	3	2		103	Sax (1928)
"	44	18	27	12	4	6	1	6		118	Kihara,W. and Y.(1933)
Total	88	43	46	22	12	9	4	8		232	
F ₁ x 6x	7	3	6	6	6	5	0	1		34	Thompson and C.(1928)
"	6	3	3	11	22	21	6	1		73	Kihara,W. and Y.(1933)
Total	13	6	9	17	28	26	6	2		107	

To sum up, the results do not show much consistency. The majority of cases show selective functioning ability between certain gametes and elimination of other infertile combinations. In some cases the differences in the transmission of chromosomes through the male and female are quite clear.

B. CHEMICAL

Technology is playing an increasingly important role in the development of new varieties. Craig and Murty (7) investigated the application of gas-liquid-phase-chromatography for the analysis of saturated and unsaturated fatty acids. Craig (6) emphasized the need of its application as an aid to plant breeding. The use of gas-liquid-phase-chromatography made possible the screening of large numbers of seed samples for desirable fatty acid components which largely determine the quality of oil for different purposes. This rapid screening led to the isolation of strains of rape with seed oil free of erucic acid from the variety Liho (42). Later on strains free of erucic acid were also isolated from B. napus obtained from Budapest. The studies on inheritance of erucic acid content showed that it is conditioned by two independent gene loci and dosage effect of the genes is additive. The effect of pollen source which influenced the composition of the oil indicated an xenia effect (13,41). In B. campestris Dorrel and Downey (8) have discovered that erucic acid is controlled by a single gene which shows incomplete dominance.

This type of research shows promise for the development of rape varieties with seed oil more competitive with other oil-seeds. Knowledge of the transfer of chromosomes and genes such as the genes for low erucic acid content in crosses between B. napus and B. campestris may assist in the development of improved seed oils.

MATERIALS AND METHODS

The seed of the Brassica species employed for these investigations was obtained from the Plant Science Department of the University of Manitoba. These species are described morphologically in Table IV and their fatty acid composition in Table V.

For the sake of brevity species B. napus L. (zero-erucic acid), B. campestris L. var oleifera Metzg. and B. campestris L. ssp. trilocularis (Roxb.) Olsson will henceforth be referred to as B. napus, B. campestris and B. trilocularis respectively.

The transmission of chromosomes in interspecific crosses of Brassica was studied in the reciprocal backcrosses of the F_1 hybrids with each parent species. In the backcross when the F_1 was used as a female parent the number of chromosomes carried by the male gamete was known and when the F_1 was used as a male parent the number of chromosomes supplied through the female gamete was known. Thus, the chromosome transmission through the male and female gametes of F_1 crosses was determined. The following single and backcrosses were made:

Interspecific crosses and their reciprocal.

B. napus x B. campestris

B. napus x B. trilocularis

TABLE IV. Morphological description of the species employed as parents.

Species	Common name	Level of ploidy	Nature of compatibility	No. of chromosomes (2n)
<u>B. napus</u> L.	Summer rape	Allotetra-ploid	Self-compatible	38
<u>B. campestris</u> L. var. <u>oleifera</u> Metzg.	Turnip rape	Diploid	Self-incompatible	20
<u>B. campestris</u> L. ssp. <u>trilocularis</u> (Roxb.) Olsson	Yellow-seeded sarson	Diploid	Self-compatible	20

TABLE V. Fatty acid composition of seed oils from
the species employed as parents.

Species	Fatty acids as per cent of total acids				
	Palmitic	Oleic	Linoleic	Linolenic	Eicosenoic Erucic
<u>B. napus</u>	5.0	62.0	23.5	8.0	1.5 0
<u>B. campestris</u>	2.9	34.0	17.6	9.0	12.8 22.5
<u>B. trilocularis</u>	1.0	12.6	13.5	9.5	5.0 55.0

Backcrosses.

B. napus x F₁ (B. campestris x B. napus)

F₁ (B. campestris x B. napus) x B. napus

B. campestris x F₁ (B. napus x B. campestris)

F₁ (B. napus x B. campestris) x B. campestris

F₁ (B. napus x B. trilocularis) x B. trilocularis

B. napus x F₁ (B. napus x B. trilocularis)

In the hybrids between B. trilocularis and B. napus when B. trilocularis was used as a female parent and B. napus as a male parent no seed was obtained as a result of ovule abortion. During the first two weeks the pods and ovules looked normal but at a later date the ovules collapsed. Therefore, only six of the possible eight F₁ backcrosses could be studied.

A fairly large number of florets were cross-pollinated to provide adequate populations. All the crossing was done in the greenhouse (72 to 85°F) where conditions were quite favourable and permitted crossing throughout the day. The florets ready to open in a three days period were emasculated and fertilized with fresh pollen obtained from a bagged inflorescence. Every possible precaution was exercised to avoid pollen contamination. Paper bags (No.317 "Central States Pollinating Bags") of size 3 x 8 inches were used to protect the inflorescences.

The F₁ seeds were planted in 7-inch pots and the F₁ plants

examined cytologically. All the F_1 plants were found to be hybrids and were subsequently backcrossed to the parent species.

For the determination of chromosome numbers in the backcross progeny of these crosses the seeds were germinated in vermiculate. Root tips were collected in water for cold treatment ($0-2^{\circ}\text{F}$) for 24 hours and fixed in a solution of ethyl alcohol (95%), chloroform and glacial acetic acid (6:3:2) and were left there for two days before cytological examination. The collection of both roots and leaves was considered advantageous for ensuring counts. The seedlings were planted in 4-inch pots, one seedling per pot. The pots were numbered and kept in growth cabinet run at about 75°F . In cases where the chromosome numbers could not be obtained from roots already collected, young leaves and healthy fast growing roots were again excised, pretreated and fixed as above. The samples were hydrolysed in N HCl for 10-12 minutes at 60°C and stained in Feulgen for about 45 minutes. The root tips and small leaf samples taken along the basal margin of the leaf were squashed in aceto-carmin. This schedule was found quite suitable for both leaves and roots as it produced bright staining and good chromosome spreads. Generally better spreads were obtained from root-tips than from leaves. Photographs were made mostly from fresh slides while some were taken from permanent slides.

For the study of meiosis of the parents and F_1 plants of different crosses, buds were collected in Carnoy's fluid and

anthers squashed in aceto-carmin. Pollen fertility was also studied by staining the pollen grains in aceto-carmin, those which remained unstained were considered to be sterile.

Gas-liquid-phase-chromatography (G.L.P.C.) was used to determine fatty acid composition of seed oil. The methods used were outlined by Stefansson and Hougen (41).

RESULTS

A. CYTOLOGICAL STUDIES

(a) Cytology of the Parents

These investigations involved three parent species B. campestris, B. trilocularis, and B. napus. The following observations were made:

(i) B. campestris. This species showed quite regular meiotic behaviour. Ten bivalents were invariably counted at metaphase (Plate I; No.1). The bivalents disjoined regularly. The somatic chromosome count was $2n=20$ (Plate I; No.2). These results confirm the findings of previous workers (1,29,39).

(ii) B. trilocularis. The meiotic behaviour of this species was also regular. Ten bivalents were counted at metaphase which disjoined regularly at first anaphase (Plate I; No.3). The somatic chromosome count was $2n=20$ (Plate I, No.4). These results are in agreement with those of Alam (1) and Sikka (39).

(iii) B. napus. The presence of 19 bivalents was confirmed at both diakinesis and metaphase (Plate I; No.5). The bivalents disjoined regularly. The entire meiotic course was regular. The somatic chromosome count was $2n=38$ (Plate I; No.6). These results confirm the early findings of U (46) and Howard (14).

PLATE I. Meiotic and somatic chromosomes of the parent species.

No.1 Meiotic metaphase showing 10^{II} in
B. campestris.

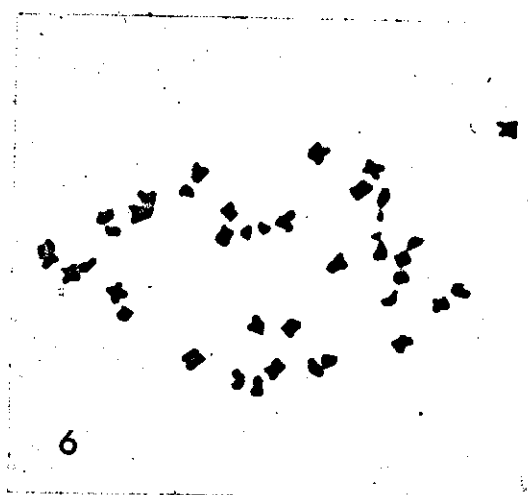
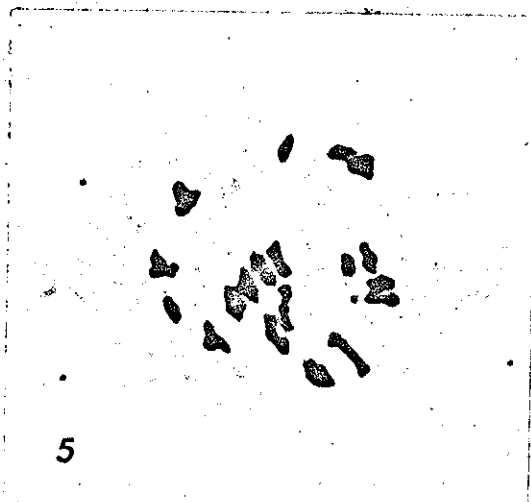
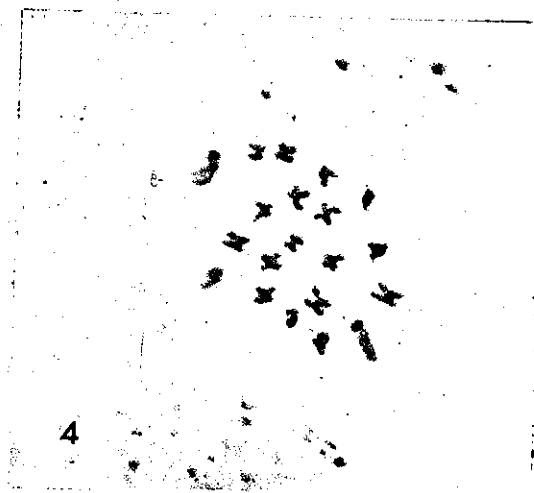
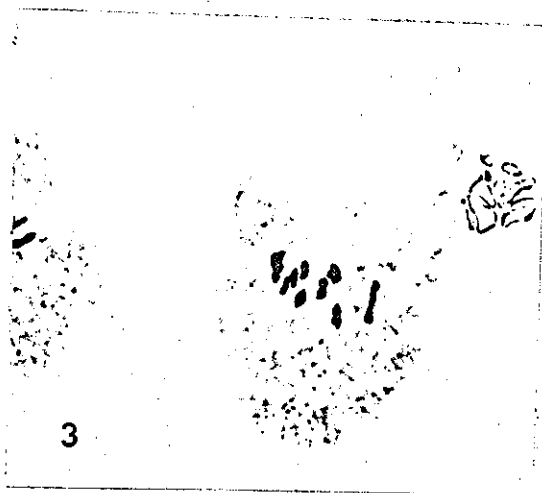
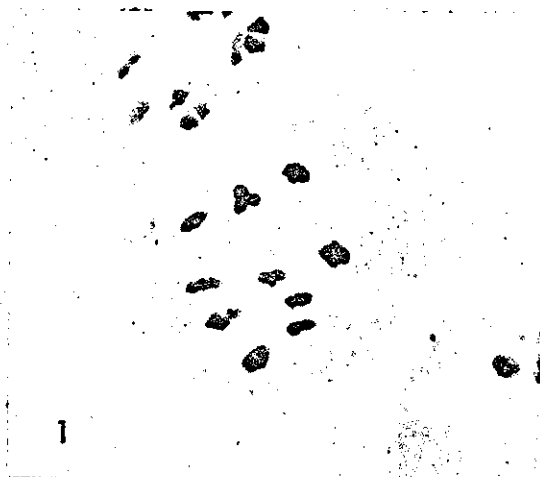
No.2 Mitotic metaphase, $2n = 20$ in
B. campestris.

No.3 Meiotic metaphase showing 10^{II} in
B. trilocularis.

No.4 Mitotic metaphase, $2n = 20$ in
B. trilocularis.

No.5 Meiotic metaphase showing 19^{II} in
B. napus.

No.6 Mitotic metaphase, $2n = 38$ in
B. napus.



(b) Cytology of F₁ Hybrids.

The cytological studies involved the following F₁ inter-specific hybrids:

B. campestris x B. napus

B. napus x B. campestris

B. napus x B. trilocularis

B. napus, one of the parents in all the three crosses is an allotetraploid (aacc) while the other two parents B. campestris and B. trilocularis are diploid species (aa). The aa genome which is common to both parents showed complete pairing while the members of the c genome appeared as univalents. At metaphase all the three hybrids showed $10^{II} + 9^I$ (Plate II; No.1). The bivalents disjoined regularly while the univalents were apparently distributed at random. The bivalents were the first to disjoin and move to the poles then the bivalents were followed by univalents. The univalents which happened to be present on the equator were seen to divide and migrate to the poles. Very frequently the univalents were found to lag at first anaphase and quite often at second anaphase. Sometimes all the nine univalents were observed at the equator while the bivalents had disjoined and reached the poles. The univalents which happened to lie away from the equator did not show signs of division and were possibly not included in the anaphase nucleus. The behaviour of univalents is illustrated

PLATE II. Univalent behaviour in the F_1 (B.campestris x B.napus) and somatic complement of F_1 (B.napus x B. trilocularis).

No.1 Meiotic metaphase showing $10^{II} 9^I$.
(Arrows indicate univalents).

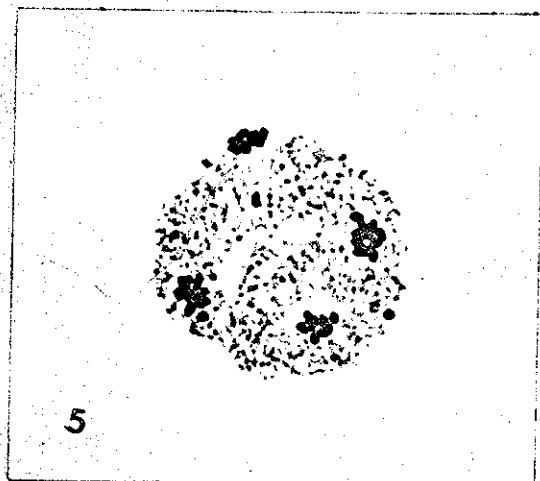
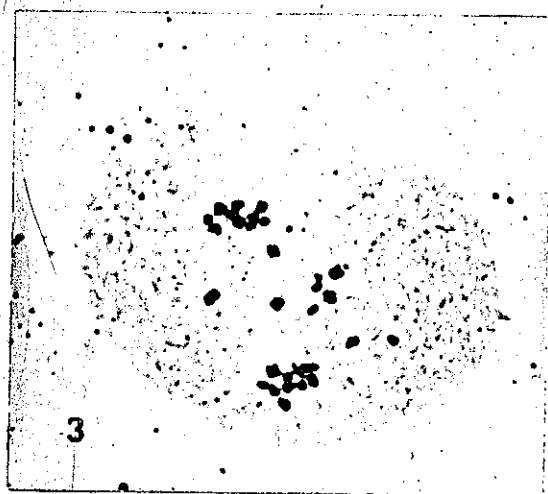
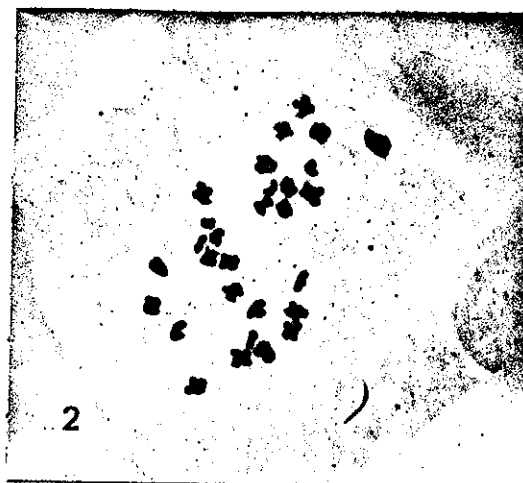
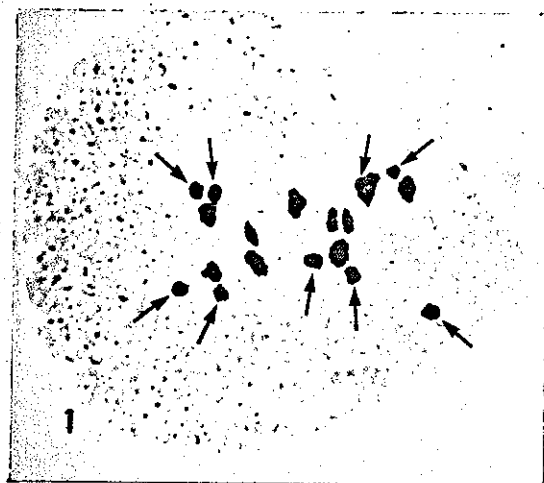
No.2 Mitotic cell showing $2n = 29$.

No.3 Anaphase I in cell with $10^{II} 9^I$. The
nine univalents have lagged at plate.

No.4 Six lagging univalents dividing at
anaphase I. At the two poles are 10
and 13 dyads, respectively.

No.5 Lagging univalents at anaphase II.

No.6 Lagging and dividing univalents at
anaphase II.



in Plate II Nos. 3 to 6. The data pertaining to the distribution of univalents at first anaphase are shown in Table VI.

From the data given in Table VI it is obvious that in the three crosses the mean distributions of univalents (4.39, 4.57, 4.22) were quite close to that of theoretical mean of 4.5. All the classes were obtained with the exception of extremes which apparently were not recovered due to low expected frequency and insufficient sample size. The chi-square values of 8.39 and 4.55 obtained for F_1 (B. campestris x B. napus) and its reciprocal respectively indicate that the distribution of univalents is random. The chi-square value of 27.43 obtained for F_1 (B. napus x B. trilocularis) indicates that the observed univalent distribution does not fit the distribution expected from random distribution of nine univalents. This may be due to the fact that the genome contributed by B. trilocularis is less closely related to B. napus than the genome from B. campestris.

The frequency of lagging of the univalents at first anaphase and telophase has been presented in Table VII. From these data it is clear that the highest frequency of PMCs has one lagging univalent followed by those with two and three lagging univalents, the frequency of PMCs with nine univalents being the lowest. The mean numbers of lagging univalents were 3.59 and 2.01 for F_1 (B. campestris x B. napus) and its reciprocal respectively and 1.57 for the

TABLE VI. Frequency distribution of univalents at first anaphase in F₁ hybrids from interspecific crosses in Brassica.

Cross	Frequency of cells with univalents										Total	Mean	S.E.	χ^2 d.f. = 5
	0	1	2	3	4	5	6	7	8	9				
F ₁ (<u>B. campestris</u> x														
<u>B. napus</u>)	1	4	12	12	25	26	15	10	2	0	107	4.39	0.163	8.397 N.S.
F ₁ (<u>B. napus</u> x														
<u>B. campestris</u>)	0	2	8	12	24	22	10	6	4	2	90	4.57	0.180	4.559 N.S.
F ₁ (<u>B. napus</u> x														
<u>B. trilocularis</u>)	0	10	4	29	44	59	11	2	4	0	163	4.22	0.108	27.432**

N.S. = not significant

TABLE VII. Frequency distribution of lagging univalents at first anaphase and telophase in F₁ hybrids from interspecific crosses in Brassica.

Cross	Frequency of cells with lagging univalents									Total	Mean	S.E.
	1	2	3	4	5	6	7	8	9			
F ₁ (<u>B. campestris</u> x <u>B. napus</u>)	66	33	29	16	18	24	21	12	5	224	3.59 ^a	0.163
F ₁ (<u>B. napus</u> x <u>B. campestris</u>)	56	34	16	6	5	2	0	0	1	120	2.01 ^b	0.124
F ₁ (<u>B. napus</u> x <u>B. trilocu-laris</u>)	29	8	6	2	0	0	0	0	0	45	1.57 ^b	0.132

Any two figures in this column which do not carry the same superscript are significantly different.

F₁ (B. napus x B. trilocularis). The mean of 3.59 univalents differed significantly from means of 2.01 and 1.57 whereas the means of 2.01 and 1.57 are not significantly different from one another. Thus, the higher frequency of univalents in male gametes from F₁ plants when B. campestris was used as the female parent indicates that the maternal parent may influence the degree of lagging of univalents.

From the data presented in Table VI regarding the distribution of univalents it is obvious that the frequencies of gametes in intermediate classes are greater than the frequencies in the extremely low and high classes. However, the frequency of PMCs with 1 to 5 lagging univalents is greater than the frequency of PMCs with the high numbers of lagging univalents, i.e. 6 to 9.

(c) Chromosome Transmission

The chromosome transmission through the male and female was investigated by somatic chromosome counts in six backcross populations derived from three parental species. The results of backcrosses of F₁ hybrids with parents along with the expected frequencies based on random distribution are presented in Tables VIII and IX. The results of transmission studies are as follows:

B. napus x F₁ (B. campestris x B. napus)

The chromosome counts made on the progeny of this backcross provide information regarding the functioning ability of male gametes.

TABLE VIII. Frequency distribution of chromosome numbers in the backcross progeny of interspecific crosses in Brassica.

Cross	Frequency	Frequency of progeny with chromosomes											χ^2	d.f.
		29	30	31	32	33	34	35	36	37	38			
<u>B. napus</u> x <u>F₁ (<u>B. campestris</u> x <u>B. napus</u>)</u>	expected	0.2	1.4	5.6	13.1	19.7	19.7	13.1	5.6	1.4	0.2			
	observed	0	2	4	12	12	20	8	19	2	1	35.83**	5	
<u>F₁ (<u>B. campestris</u> x <u>B. napus</u>)</u> x <u>B. napus</u>	expected	0.1	1.3	5.3	12.5	18.7	18.7	12.5	5.3	1.3	0.1			
	observed	4	8	16	16	6	12	7	6	0	1	80.11**	5	
<u>B. napus</u> x <u>F₁ (<u>B. napus</u> x <u>B. trilocularis</u>)</u>	expected	0.1	0.6	2.5	5.7	8.6	8.6	5.7	2.5	0.6	0.1			
	observed	0	0	6	1	6	5	1	9	5	2	10.12*	3	
Total		4	10	26	29	24	37	16	34	7	4			

Chromosome counts were made on 81 plants of the backcross progeny. With the exception of the 29 chromosome class all other chromosome classes (30 to 38) expected from random distribution of nine univalents were obtained. The extreme classes were represented by small numbers of plants and the intermediate classes (31 to 36) by a large number of plants. The results are shown graphically in Fig.1.

The chi-square value of 35.83 indicates a non-random distribution. This discrepancy is the result of an excess in the 36 chromosome class and a deficiency in the 33 and 35 chromosome classes. One plant had a somatic chromosome number of 45. This was probably the result of fertilization by an unreduced gamete from the male parent and a normal gamete from the female parent.

The morphology of the seed pods of all the plants with different chromosome numbers in the backcross progeny was examined. Few seeds were formed in pods of plants with several univalents while many seeds were formed in pods of plants with few or no univalents. The pods with poor seed set were very much constricted and no seed was formed at the places of constriction. Individual seeds were formed in the expanded portions. The pods with good seed set were more or less uniform throughout their length and resembled those of the euploid parents (Plate IV). In the cross plants in the low chromosome classes generally contained more univalent chromosomes, than those in the high chromosome classes. Thus this appearance of the pods could probably be used to

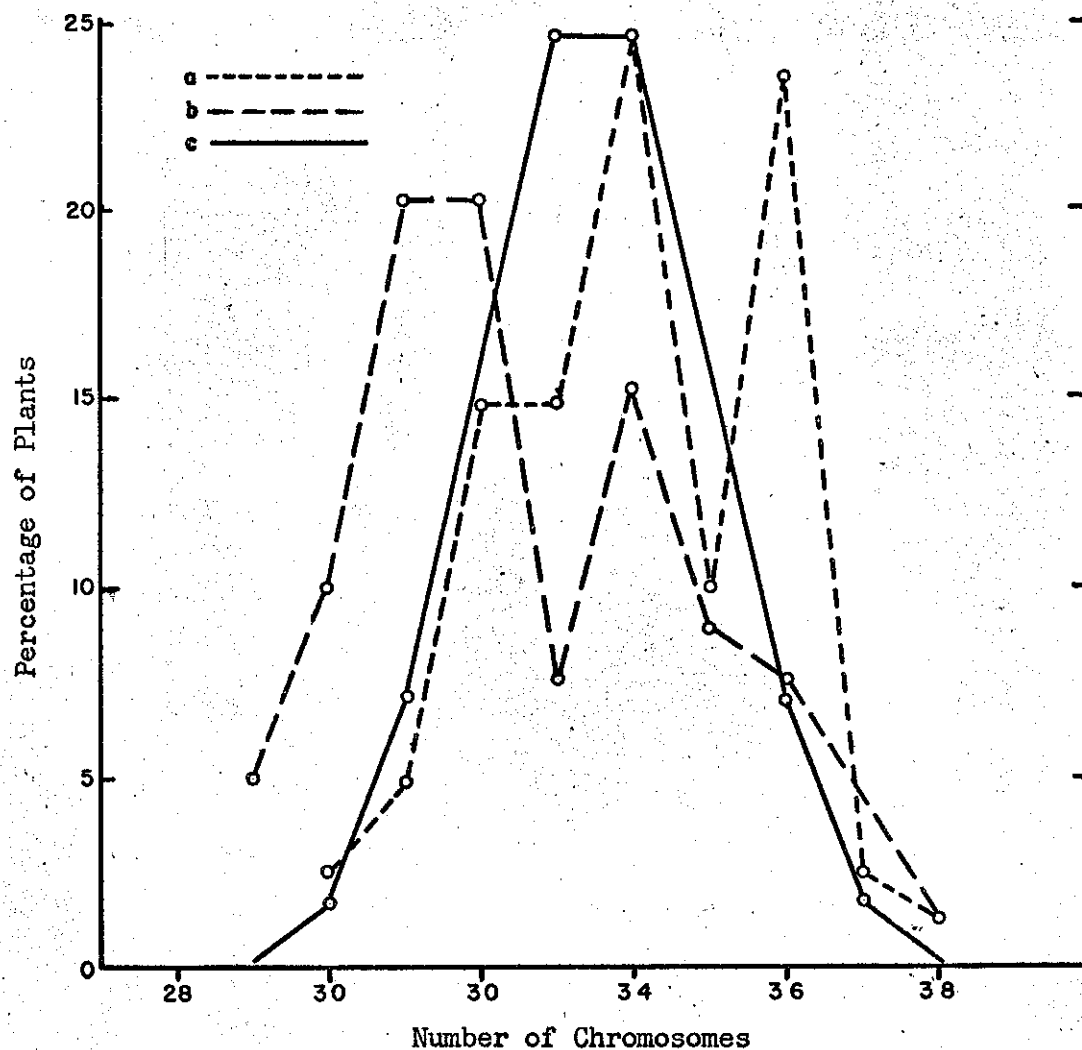


FIGURE 1. Frequency distribution of chromosome numbers in the backcross progeny of; a, B. napus x F₁ (B. campestris x B. napus); b, F₁ (B. campestris x B. napus) x B. napus; c, theoretical.

PLATE III. Typical somatic chromosome complements in the F_1 of the cross or its reciprocal (B. napus x diploid) x B. napus.

No.1 $2n = 36$
No.2 $2n = 35$
No.3 $2n = 34$
No.4 $2n = 33$
No.5 $2n = 32$
No.6 $2n = 30$

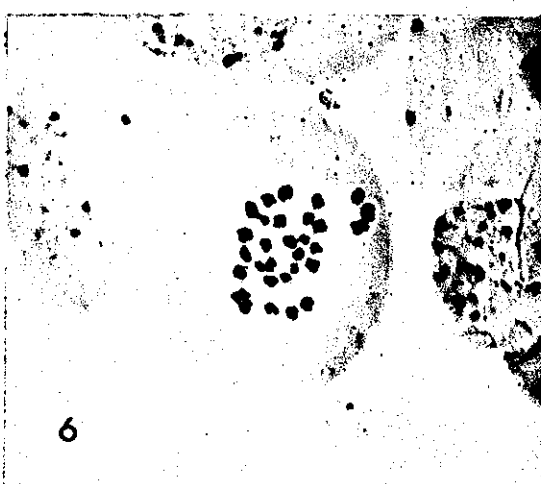
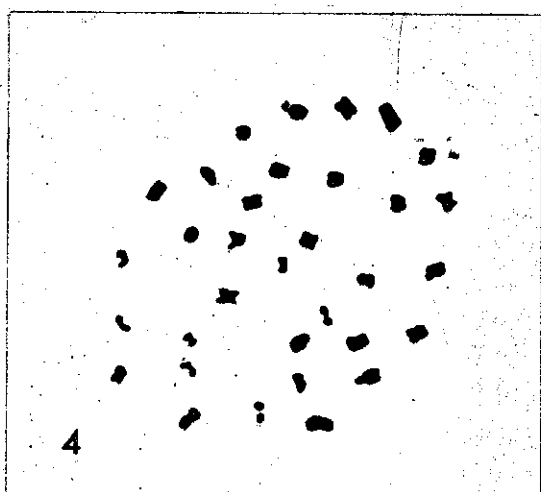
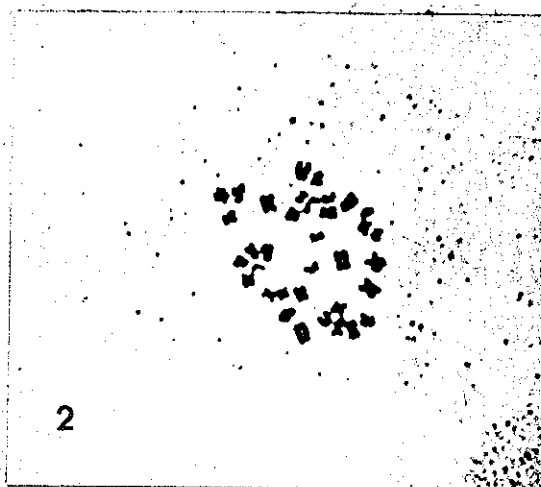


PLATE IV. Typical pod characteristics of F_1 plants
from the cross B. napus x F_1 (B. campestris x
B. napus) illustrating the effect of aneuploidy
on seed set. Chromosome numbers are shown below
pods.



34



33



32



31



30



45



38



37



36



35

distinguish those plants whose chromosome number approached that of the parent with the higher chromosome number.

F₁ (B. campestris x B. napus) x B. napus

Since the F₁ was used as the female parent in this backcross, the chromosome numbers of the progeny provide information on the functional gametes derived from the female. The chromosome numbers were determined on a population of 79 plants. With the exception of the 37 chromosome class all expected chromosome numbers were recovered in the progeny. The absence of the 37 chromosome plants is probably due to chance as the expected frequency for this class was quite low (1.3 plants). The chromosome numbers of 82.89% of the plants ranged from 31 to 36. Although the chromosome numbers in the majority of the plants were intermediate, the chi-square test ($\chi^2 = 80.11$) indicated a very significant deviation from the distribution expected from random distribution of univalents. This deviation was primarily due to deficiencies in the 33, 34 and 35 chromosome classes and an excess in the 30 and 31 chromosome groups. Three plants with somatic chromosome number of 45 were recovered. These plants probably developed from the combination of unreduced female gametes and normal male gametes.

The appearance of the pods in different chromosome classes followed a pattern similar to the one shown for the previous cross. However, the differences were comparatively less marked since the



poor growing conditions towards maturity tended to obscure the variations in seed set which were associated with a high number of univalents.

B. napus x F₁ (B. napus x B. trilocularis)

The genome of B. trilocularis differs from the 10 chromosome genome used in the previous two crosses. Chromosome numbers were determined on 36 F₁ plants of the backcross progeny. The chromosome numbers in this cross ranged from 31 to 38. The lower classes of 29 and 30 were not recovered probably due to the low expected frequencies of 0.1 and 0.6 for the 29 and 30 chromosome classes. Again 80.0% of the total plants examined fell in the intermediate group of 31 to 36 chromosomes. The results are shown graphically in Fig.2. The chi-square value of 10.12 obtained indicates a non-random distribution of univalents. This discrepancy resulted from an excess of plants in classes with relatively low expected frequencies at both the extremes. One plant with a somatic chromosome number of 49 was probably the result of the union of an unreduced gamete from the male and a normal gamete from the female parent.

In the three backcrosses already reported the F₁ was backcrossed to B. napus and the expected chromosome range based on the

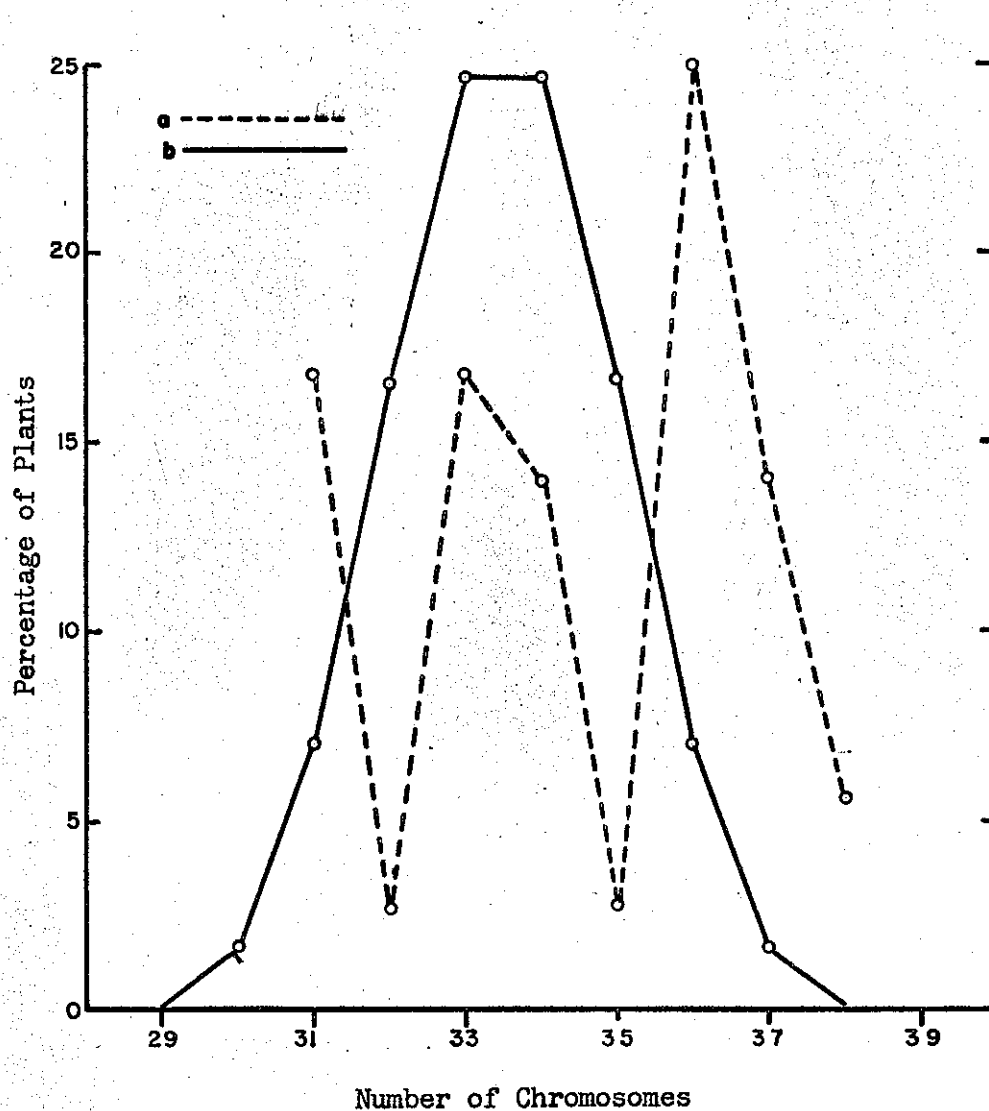


FIGURE 2. Frequency distribution of chromosome numbers in the backcross progeny of; a, *B. napus* x *F1* (*B. napus* x *B. trilocularis*); b, theoretical.

random distribution of nine univalents was 29 to 38. In the remaining three crosses which are reported in the following pages the F_1 was backcrossed to diploid parent species ($n=10$). The expected chromosome range in this case is 20 to 29 chromosomes. The data pertaining to three such crosses are reported in Table IX.

B. campestris x F_1 (B. napus x B. campestris)

In this backcross the F_1 is the male parent and furnishes information on the functional male gametes. The frequency of plants in chromosome classes of 24 and 25 is quite low and high in chromosome class of 21. As a consequence the chi-square value of 21.27 indicates deviation between the observed and expected distributions based on random distribution of univalents. Plants were recovered in all the expected chromosome classes. Most of the plants (75.51%) were in the intermediate chromosome group of 22 to 27 chromosomes. One plant had 18 chromosomes. This is lower than the lowest expected number of 20 chromosomes and was the only case where a plant with less than 20 chromosomes was obtained (Fig.3).

F_1 (B. napus x B. campestris) x B. campestris.

The F_1 was used as a female parent to observe the transmission of chromosome numbers through the female gametes. All the expected chromosome classes with the exception of the 28 chromosome class were recovered. The frequency of plants with intermediate chromosome

TABLE IX. Frequency distribution of chromosome numbers in the backcross progeny of interspecific crosses in Brassica.

Cross	Frequency	Frequency of progeny with chromosomes										χ^2	d.f.
		20	21	22	23	24	25	26	27	28	29		
<u>B. campestris</u> x <u>F1 (B.napus x</u> <u>B. campestris</u>	expected	0.1	0.9	3.4	8.0	12.1	12.1	8.0	3.4	0.9	0.1		
	observed	1	9	5	9	5	4	9	5	1	1	21.27**	3
<u>F1 (B.napus x</u> <u>B. campestris)</u> x <u>B. campestris</u>	expected	0.1	1.2	4.9	11.3	17.0	17.0	11.3	4.9	1.2	0.1		
	observed	2	7	5	13	15	12	6	6	0	3	15.53**	5
<u>F1 (B.napus x</u> <u>B. trilocularis)</u> x <u>B. trilocularis</u>	expected	0.1	1.1	4.2	9.8	14.8	14.8	9.8	4.2	1.1	0.1		
	observed	3	10	7	14	8	12	2	3	0	1	51.59**	5
Total		6	26	17	36	28	28	17	14	1	5		

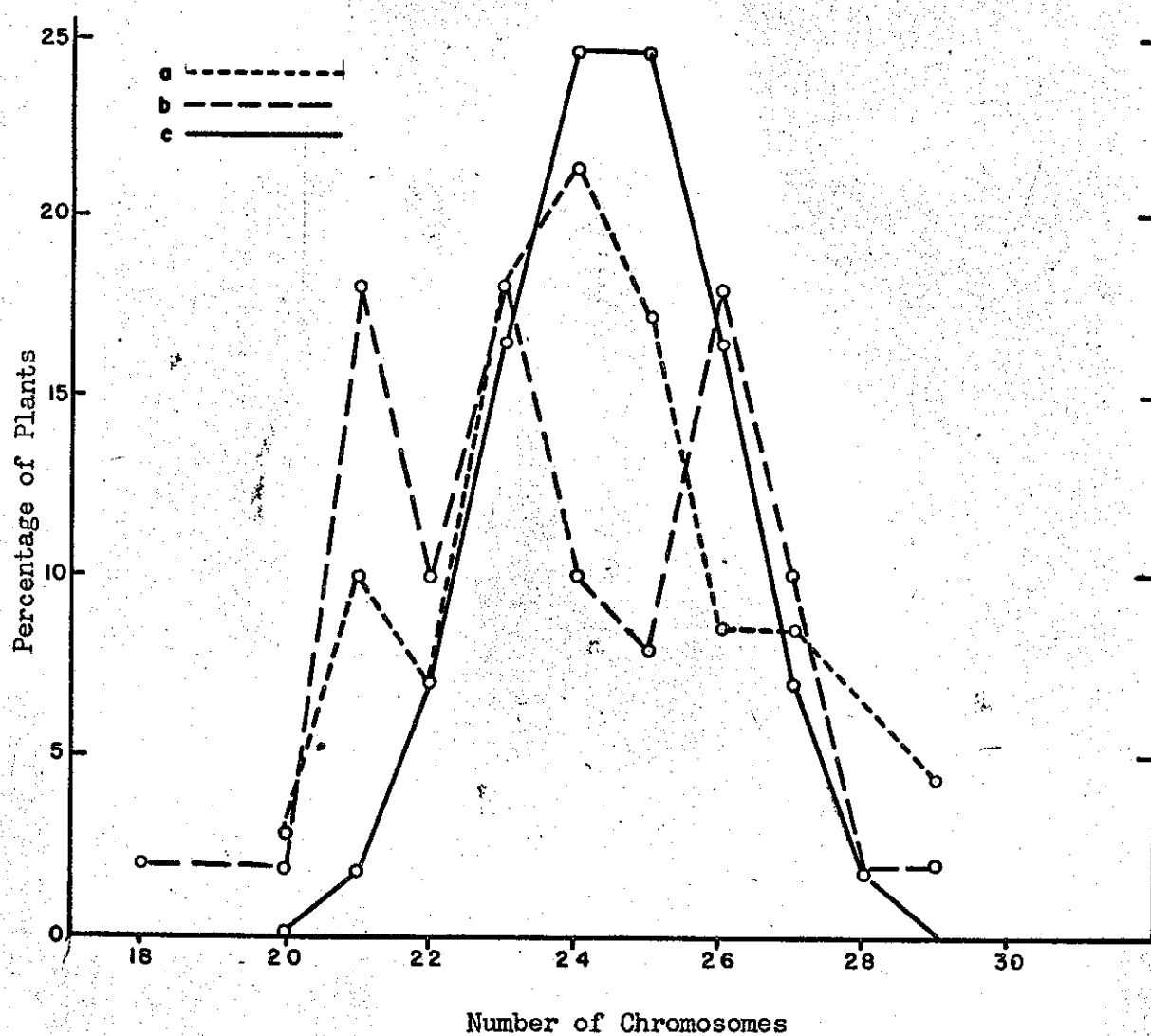


FIGURE 3. Frequency distribution of chromosome numbers in the backcross progeny of; a, B. campestris x F_1 (B. napus x B. campestris); b, F_1 (B. napus x B. campestris) x B. campestris; c, theoretical.

numbers (22 to 27) was 82.60%. The chi-square value of 15.53 does not indicate good fit between the observed and expected distributions based on random distribution of univalents. The deviation is the result of an excess in the 21 chromosome class and a deficiency in the 25 and 26 chromosome classes (Fig.3). The somatic chromosome number of one plant was 40. This plant probably developed from an unreduced gamete from the F_1 and a normal gamete from the male parent.

F_1 (B. napus x B. trilocularis) x B. trilocularis

The data obtained from this cross again shows transmission of chromosomes from the F_1 employed as a female parent. With the exception of the 28 chromosome class all other classes expected from random distribution were obtained. This class was not recovered due to the low expected frequency (1.1) in this class. However, the plants with intermediate chromosome numbers (22 to 27) occurred in the high frequency of 76.66%. The results are graphically shown in Fig.4. The high chi-square value of 51.59 shows a significant deviation from the distribution expected from random distribution of univalents. The discrepancy is the result of an excess of plants in classes with low chromosome numbers and a deficiency in the 24 and 26 chromosome classes.

In the backcrosses of F_1 to the 10 chromosome species the frequency of plants in the intermediate group was also higher (78.65%)

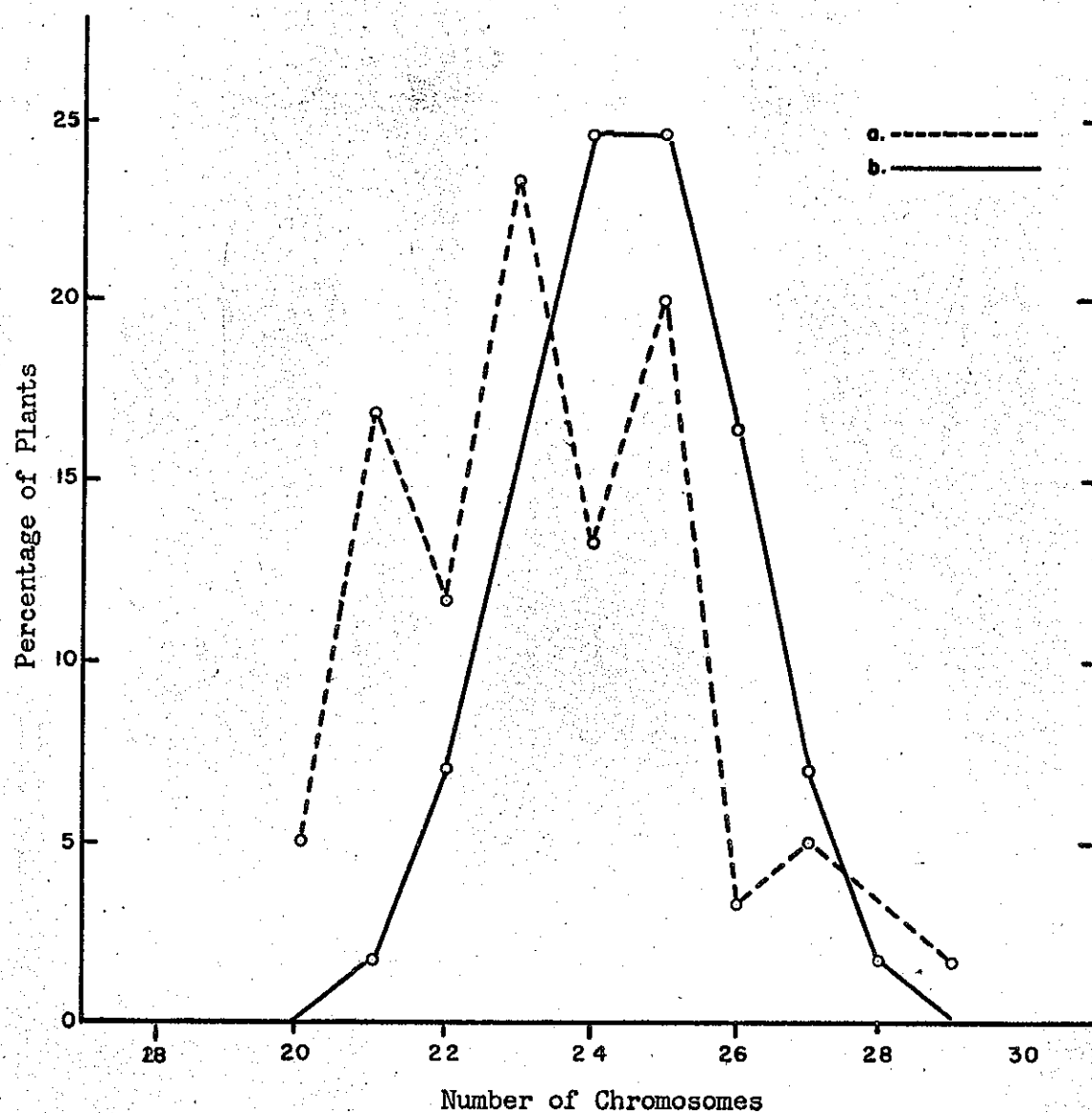


FIGURE 4. Frequency distribution of chromosome numbers in the backcross progeny of; a, F_1 (B. napus x B. trilocularis) x B. trilocularis; b, theoretical.

PLATE V. Figs. 1-4. Typical somatic chromosome complements observed in F_1 of the cross or its reciprocal (B.napus x diploid species) x diploid species.

No.1 $2n = 21$

No.2 $2n = 22$

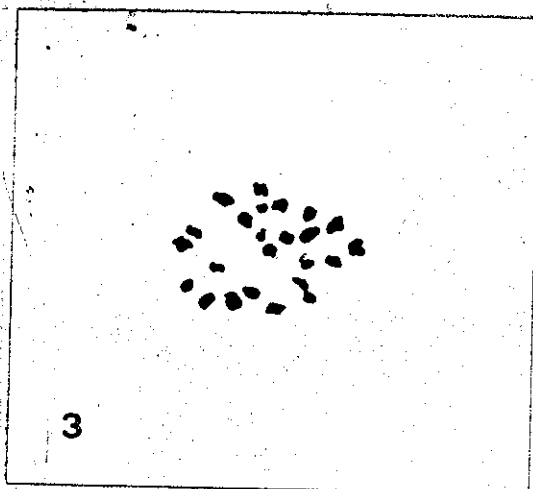
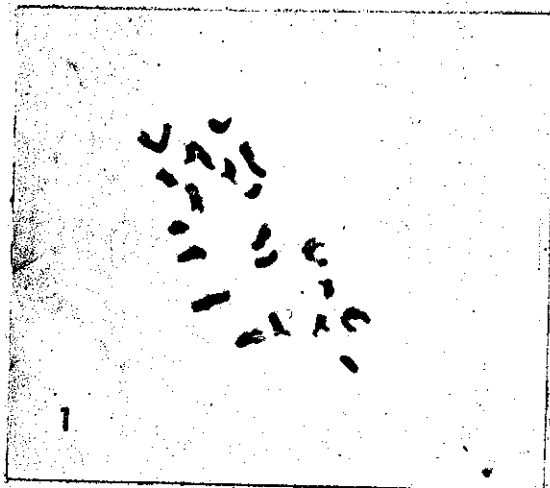
No.3 $2n = 24$

No.4 $2n = 28$

Nos.5 and 6. Aberrant chromosome complements.

No.5 $2n = 18$ (from above cross)

No.6 $2n = 49$ (from B.napus x F_1 (B.napus x diploid))



than the frequencies of plants in high (3.37%) and low classes (17.97%). The functioning ability of gametes with low chromosome numbers was better than that of the gametes with high chromosome numbers.

(d) Pollen Fertility

Pollen fertility was studied in five out of the six backcrosses. The data for the two crosses with a chromosome range of 29 to 38 are shown in Table X and those of the other three crosses with a chromosome range of 20 to 29 are given in Table XI. In the progeny of the cross of the F_1 and the parent with the higher chromosome number ($n=19$), low chromosome number and low pollen fertility were associated. The pollen fertility for 29, 30, 31 and 32 chromosome plants was 60.6, 52.5, 56.3 and 63.4% respectively, whereas the pollen fertility for chromosome classes of 33 to 38 ranged from 76.0 to 81.0%. The pollen fertility for the aberrant plants was 48.0% for the plant with 45 chromosomes and 83.5% for the one with 49 chromosomes.

In the remaining three backcrosses where the backcross parent was the 10 chromosome species, the classes with low chromosome numbers gave better pollen fertility than the plants in intermediate and high chromosome classes. The range of pollen fertility was from 85.4% (20 chromosomes) to 37.0% (29 chromosomes).

TABLE X. The mean percentage pollen fertility in the backcross progeny of interspecific crosses in Brassica.

Cross	Mean pollen fertility in progeny with chromosomes											
	29	30	31	32	33	34	35	36	37	38	45	49
<u>F₁</u> (<u>B. campestris</u> x <u>B. napus</u>) x <u>B. napus</u>	60.6	52.5	64.1	68.5	79.3	70.3	81.0	75.6	-	77.0	48.0	-
<u>B. napus</u> x <u>F₁</u> (<u>B. napus</u> x <u>B. trilocularis</u>)	-	-	48.5	58.4	82.4	81.8	-	85.8	80.7	83.5	-	83.5
Mean	60.6	52.5	56.3	63.4	80.8	76.0	81.0	80.7	80.7	80.2		

TABLE XI. The mean percentage pollen fertility in the backcross progeny of interspecific crosses in Brassica.

Cross	Mean pollen fertility in progeny with											
	18	20	21	22	23	24	25	26	27	28	29	40
chromosomes												
<u>B. campestris</u> x	85.2	94.0	72.2	85.3	69.9	56.0	45.1	53.7	54.7	53.5	29.3	-
<u>F₁ (B.napus x</u>												
<u>B. campestris)</u>												
<u>B. campestris</u>												
<u>F₁ (B.napus x</u>	-	99.6	79.8	67.5	70.1	59.0	54.5	55.0	67.7	-	64.4	93.7
<u>B. campestris)</u>												
<u>B. campestris</u>												
<u>F₁ (B.napus x</u>												
<u>B. trilocularis) x</u>												
<u>B. trilocularis</u>	-	62.8	75.3	86.6	65.5	68.6	49.2	53.7	65.4	-	17.26	-
<u>B. trilocularis</u>												
Mean	85.4	75.7	79.8	68.5	61.2	49.6	54.1	62.6	53.5	37.0		

B. CHEMICAL STUDIES

The chemical studies deal with the inheritance of erucic acid contents in rapeseed oil. The two species involved are B. campestris a diploid species and B. napus an amphidiploid of B. campestris and B. oleracea. The fatty acid composition of the parent species is given in Table V. The seed oil from amphidiploid species B. napus is free of erucic acid while erucic acid content for the diploid species B. campestris is about 22%.

The fatty acid composition of the seed oil from the ten plants from backcross progeny of B. napus x F₁ (B. campestris x B. napus) was determined. The data pertaining to fatty acid composition are reported in Table XII. The erucic acid contents ranged from 0 to 7.5%. The seed oil from four of the ten plants was free of erucic acid, while the seed oil from the other six plants contained small percentages of erucic acid varying from 4.1 to 7.5%. Recovery of four plants with seed oil free of erucic acid and six plants with seed oil containing erucic acid probably represents 1:1 ratio expected from a backcross on the basis of single gene difference. The low values of erucic acid in the F₁ backcross which has chromosome numbers from 36 to 38 may be attributed to dilution of the effects of the gene from B. campestris in the presence of both the aa and cc genomes. A gene for the production of erucic acid in B. campestris has been transferred to B. napus which was free of

TABLE XII. Fatty acid composition of seed oils from the
F₁ progeny of the cross B. napus x F₁ (B. cam-
pestris x B. napus).

Plant No.	No. of Chromosomes (2n)	Fatty acids as per cent of total acids				
		Palmitic	Oleic	Linoleic	Linolenic	Eicosenoic
35	38	4.8	56.0	16.1	8.3	11.3
2	37	3.9	69.0	19.2	5.6	2.2
13	37	5.7	58.2	13.8	6.0	11.8
6	36	4.3	71.0	14.7	7.1	2.7
14	36	4.6	70.2	16.5	7.3	1.4
15	36	5.1	48.7	17.8	7.9	13.6
21	36	5.0	71.1	15.0	6.6	2.2
24	36	4.8	52.6	15.3	6.8	12.9
31	36	5.7	50.5	18.3	7.8	10.2
34	36	4.7	57.5	14.0	6.3	12.0

erucic acid. The results of these studies are in agreement with the findings of Dorrel and Downey (8) that the production of erucic acid in B. campestris is controlled by a single gene.

DISCUSSION AND CONCLUSIONS

For the study of the chromosome transmission in interspecific crosses of Brassica, the cytological behaviour of the parent species was considered very essential which if found aberrant could influence the transmission results a great deal. The meiotic behaviour of the diploid as well as the allotetraploid species involved in these studies revealed that the meiotic course was regular as already reported by different authors such as Alam (1), Sikka (39) and others.

The distribution of the univalents belonging to the c genome contributed by B. napus to the F_1 of crosses between diploid species, B. campestris (aa) and the allotetraploid species B. napus (aacc) approached the distribution expected for random distribution of univalents.

The frequency distributions at first anaphase in the three F_1 hybrids show that there is a tendency of univalents to go to the poles in combinations of 4 and 5. This tendency thus favours the production of gametes with intermediate chromosome numbers in a greater frequency than the extremely high or low numbers. The mean numbers of univalents at first anaphase were 4.39 and 4.57 for F_1 (B. campestris x B. napus) and its reciprocal respectively and 4.22 for F_1 (B. napus x B. trilocularis). These means are quite

close to the expected mean, 4.5 for random distribution of univalents. The chi-square values of 8.39 and 4.55 obtained from a comparison of observed and expected frequencies of univalents at first anaphase in F_1 (B. campestris x B. napus) and its reciprocal respectively indicate agreement with the hypothesis of random distribution of univalents. In the F_1 (B. napus x B. trilocularis) the tendency appears to be the same favouring gametes with predominantly intermediate chromosome numbers but the chi-square value of 27.43 shows that observed frequencies deviated from the expected. The deviations obtained in this cross could be attributed to the aa genome contributed by B. trilocularis which is not so closely related to the aa genome of B. napus as the genome contributed by B. campestris. The failure of B. napus to cross with B. trilocularis as a female parent is another indication of its genomic differences from that of B. campestris. When B. napus was employed as a female parent the cross was successful.

The distribution of univalents was further influenced by their behaviour at second anaphase through their lagging and division. The frequency of gametes with different chromosomes could only be accurately observed if counts at second anaphase were possible. The observations made at first anaphase with highly irregular univalent behaviour can only present a rough idea about gamete formation. The backcrosses in addition to yielding some information about univalent behaviour furnish information on the functioning ability of certain

chromosomal combinations. The behaviour of the lagging univalents at first anaphase and telophase shows that in F_1 (B. campestris x B. napus) and its reciprocal one univalent occurs with maximum frequency of 29.46 and 46.66% followed by two univalents (14.73 and 28.33%) three univalents (12.93 and 13.33%) respectively. In the case of F_1 (B. napus x B. trilocularis) also one univalent has the maximum frequency of 64.44% followed by two univalents (17.77%), three univalents (13.33%). The mean numbers of lagging univalents were 3.59 and 2.01 for F_1 (B. campestris x B. napus) and its reciprocal respectively and 1.5 for F_1 (B. napus x B. trilocularis). The mean number of lagging univalents in the F_1 (B. napus x B. campestris) and F_1 (B. napus x B. trilocularis) where B. napus was a female parent was essentially the same. In the case of reciprocal F_1 (B. campestris x B. napus) where B. campestris was a female the means were statistically different from the other two with B. napus as a female. This indicates that the female parent may influence the degree of lagging of univalents.

The perusal of the Tables VIII and IX reveals a greater frequency of plants with intermediate chromosome numbers over those with extremely high and low numbers. Most of the expected classes based on random distribution of univalents were recovered. The failure to recover some of the extreme classes probably was a matter of chance due to low expected frequencies. Univalents at first anaphase are distributed in an approximately random manner. Distribution of chromosome numbers of plants from the F_1 of backcross progeny deviates

significantly from expected if distribution is based on chance alone. The deviations in certain chromosome classes probably are the result of selective functioning ability of certain gametic combinations, gametic and zygotic elimination etc. With a view to having an over-all picture of univalent transmission from the male and female the results of six backcrosses are reported in Table XIII. From the perusal of the table it is understood that the mean number of univalents for the six backcross populations varied around the theoretical mean of 4.5 and ranged from 3.5 to 5.4. When the transmission through the male is considered the mean univalent transmission is somewhat higher than through the female. This is true in the case of both F_1 (B. napus x B. campestris) and F_1 (B. napus x B. trilocularis) crosses. The mean univalent transmissions through the male and female in backcrosses to B. napus and B. campestris are 4.45 and 3.75 respectively.

The results of these studies confirm and extend those of Catcheside (4). His very limited observations also favoured higher transmission in intermediate numbers of univalents.

The results of Olsson (32) on chromosome transmission with haploid B. napus differ from the present findings. His results indicate that mostly the gametes with high chromosome number ($n=19$) are functional and progeny are normal diploid plants. The differences may be due to the fact that 19 univalents are present in the haploid. Those gametes which lacked homeologous chromosomes from both genomes a and c probably were inviable. Whereas in the present study one

TABLE XIII. Frequency distribution of univalents in the back-
cross progeny of interspecific crosses in Brassica.

Cross	Frequency of progeny with univalents										Mean
	0	1	2	3	4	5	6	7	8	9	
<u>B. napus</u> x F ₁ (<u>B. campestris</u> x <u>B. napus</u>)	0	2	4	12	12	20	8	19	2	1	5.00
<u>B. campestris</u> x F ₁ (<u>B. napus</u> x <u>B. campestris</u>)	1	9	5	9	5	4	9	5	1	1	3.90
Total	1	11	9	21	17	24	17	24	3	2	4.45
F ₁ (<u>B. campestris</u> x <u>B. napus</u>) x <u>B. napus</u>	4	8	16	16	6	12	7	6	0	1	3.50
F ₁ (<u>B. napus</u> x <u>B. campestris</u>) x <u>B. campestris</u>	2	7	5	13	15	12	6	6	0	3	4.00
Total	6	15	21	29	21	24	13	12	0	4	3.75
<u>B. napus</u> x F ₁ (<u>B. napus</u> x <u>B. trilocularis</u>)	0	0	6	1	6	5	1	9	5	2	5.40
F ₁ (<u>B. napus</u> x <u>B. trilocularis</u>) x <u>B. trilocularis</u>	3	10	7	14	8	12	2	3	0	1	4.00

complete genome can be expected to be present in all gametes. The complete genome can be expected to make a substantial contribution to the viability or functioning ability of most of the gametes.

The aberrant plants found in some of the crosses with chromosome numbers higher than the expected probably are the result of the union of unreduced gametes from one parent and normal gametes from the other. The presence of unreduced gametes in Brassica has been reported by a number of early authors (12,25,30).

Studies on chromosome transmission carried out in a number of other genera such as Triticum, Oenothera, Zea, Nicotiana etc., are reported in Tables II and III. In Triticum apart from one case where results favour greater transmission of intermediate chromosome numbers all others lack transmission of intermediate chromosome numbers and yield high frequencies in extreme classes thus indicating that certain chromosomal combinations are much more functional than others. When the F_1 Triticum hybrids were backcrossed to the tetraploid parent there was a preponderance of gametes with 14 chromosomes and when backcrossed to hexaploid parent there was greater transmission of gametes with 21 chromosomes.

In other Oenothera species, Zea and Nicotiana the results of chromosome transmission favour transmission of intermediate numbers while others favour extreme classes. This could possibly be the result of the different species involved in the studies. A few

genera such as Solanum, Fragaria and Petunia favour extreme classes.

In the case of Triticum pentaploid hybrids when the transmission of chromosomes through the male and female is considered the differences are not quite as well marked as in some of other species. The present investigations also do not show conspicuous differences in transmission through the male and female. However, the results on different crop species reported in Table II indicate some marked differences in transmission through the male and female gametes. In Oenothera ($3x \times 4x$) when transmission through the male is considered all the expected chromosome classes appear and results favour transmission of intermediate chromosome numbers, whereas, in case of transmission through pollen only extreme classes appear.

The results in different species show a lack of consistency. Under the circumstances it is very difficult to explain the segregation phenomenon fully. Some of the classes which show greater deviation from the expected frequencies based on random distribution probably are the result of selective functioning ability and elimination of certain gametic and zygotic combinations.

Pollen fertility was studied in the progeny of five backcrosses. The perusal of the data presented in Tables X and XI reveals that the pollen fertility is affected by the number of univalents present. In the backcrosses with the diploid species, plants with

low chromosome numbers gave higher pollen fertility, whereas, in backcrosses with allotetraploid species, plants with higher chromosome number gave better pollen fertility. As the number of univalents increased the pollen fertility decreased. Therefore, the number of univalents and pollen fertility are negatively associated.

From the results reported in Table VIII it is evident that the frequency of monosomics, double monosomics, triple monosomics from backcrosses of the F_1 with B. napus is quite high (29.84%). By the random assortment of nine univalents belonging to the c genome nine kinds of monosomics are possible. The remaining ten monosomics can possibly be produced by backcrossing the F_1 hybrid between B. napus and B. oleracea to B. napus. These monosomics will be the result of random distribution of ten univalent chromosomes belonging to the aa genome. The study of the somatic complement reveals that the morphological identification of the complement is not feasible. Only a few chromosome pairs can be identified. Thus, the identification of the monosomics by the study of pairing would be very difficult task.

The species which favour greater transmission of chromosome numbers on both extremes would attain diploidization in a relatively shorter time than those in which the chromosome transmission favours a high frequency of plants in the intermediate classes with extreme classes approaching expected numbers. Tokumasu (44) studied the collapse of tetraploidy in Raphanus sativus and concluded that

triploids, including hypo- and hyper-triploids, were the most important for the breakdown of tetraploidy. They are the first to start diploidization. When transmission of extremely high or low chromosome numbers occurs frequently, reversion to parental species will be more rapid than when intermediate chromosome numbers are transmitted with high frequency. In Brassica hybrids the frequencies of extremely high and low classes are quite low. The results of all the six crosses favour transmission of intermediate chromosome numbers. The aneuploids of Brassica will require a relatively large number of generations to revert to the parental chromosomal numbers.

SUMMARY

In the present study an attempt was made to gain knowledge of the transmission of chromosomes in interspecific crosses of Brassica.

The meiotic behaviour within the parent species is quite regular. The chromosome numbers of the diploid species is $n = 10$ and of allotetraploid species $n = 19$.

In the F_1 hybrids between allotetraploid and diploid species at metaphase ten bivalents and nine univalents were observed. The bivalents disjoined regularly and nine univalents belonging to the c genome segregated almost at random.

The mean number of univalents at first anaphase in F_1 (B. campestris x B. napus) and its reciprocal was 4.39 and 4.57 respectively and 4.22 for the F_1 (B. napus x B. trilocularis) which is quite close to the expected mean of 4.5.

The results favour transmission of gametes with intermediate chromosome numbers. Practically all of the possible chromosome classes expected from random distribution of univalents were recovered.

The mean number of univalents for the six backcross populations varied between 3.5 and 5.4. Only minor differences in frequency of transmission through the male and female were observed.

In crosses of the F_1 with B. napus the number of chromosomes is negatively associated with the number of univalents and positively associated with seed setting.

There was a negative association between pollen fertility and the number of univalents. With an increase in univalent number the pollen fertility decreased.

The frequency of monosomics, double monosomics, triple monosomics in backcross with B. napus is quite high (29.84%). Due to lack of morphological differences in the chromosomes of the complement the prospects of producing aneuploid series in B. napus are not good.

The fatty acid analysis of seed oil from ten plants from the progeny of B. napus x F_1 (B. campestris x B. napus) furnishes two distinct classes with respect to erucic acid in the ratio of almost 1:1. This is in agreement with the published results which indicate that the erucic acid in B. campestris is conditioned by a single gene. The transfer of the gene for erucic acid from B. campestris to B. napus has been achieved.

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