UNIVERSITY OF SASKATCHEWAN

UNIVERSITY OF SASKATCHEWAN

COLLEGE OF GRADUATE STUDIES

CERTIFICATION OF THESIS WORK

We, the undersigned, certify that Hans Baenziger, B.S.A.; M.Sc.

candidate for the Degree of Doctor of Philosophy

has presented his thesis on the subject, Supernumerary Chromosomes in Crested Wheat-grass, Their Cytological Behavior and Breeding Significance.

that the thesis is acceptable in form and content, and that the student demonstrated a satisfactory knowledge of the field covered by his thesis in an oral examination held on April 10, 1961

External Examiner

Professor of

Internal Examiners

-

-

-

-

-

-

-

UNIVERSITY OF SASKATCHEWAN

COLLEGE OF GRADUATE STUDIES

Summary of the Dissertation

SUBMITTED IN PARTIAL SATISFACTION

OF THE REQUIREMENTS FOR THE

Degree of Doctor of Philosophy

BY

Hans Baenziger

B.S.A. 1951, Institute of Technology, Zurich, Switzerland;
M.Sc. 1957, University of Saskatchewan.

DEPARTMENT OF FIELD HUSBANDRY

April, 1961

COMMITTEE IN CHARGE:

Prof. W. J. WHITE (*Chairman*)
Dr. R. P. KNOWLES
Prof. D. R. KNOTT
Prof. E. N. LARTER
Prof. T. J. ARNASON
Dean B. W. CURRIE

EXTERNAL EXAMINER:

Dr. R. C. McGINNIS, Plant Science Department, University of Manitoba, Winnipeg, Manitoba.

THESIS

SUPERNUMERARY CHROMOSOMES IN CRESTED WHEATGRASS, THEIR CYTOLOGICAL BEHAVIOR AND BREEDING SIGNIFICANCE.

The cytological behavior of and the effects of supernumerary chromosomes were studied in three species of crested wheatgrass, namely in diploid *Agropyron cristatum* (L.) Gaern., and in the tetraploid species *A. desertorum* (Fisch.) Schult. and *A. imbricatum* (M.B.) Roem. and Schult.

Cytological studies showed:

1. Supernumerary chromosomes occurred at meiosis in diploid and tetraploid populations of crested wheatgrass. They were absent in the diploid variety Fairway, but were present with frequencies exceeding 95 per cent in two introductions of the diploid species. In tetraploid populations their frequency ranged from 36.9 per cent to 88.5 per cent.

2. Plants of diploid S-3541 contained supernumeraries in pollen mother cells, in primary roots, and in stem tissues, but not in adventitious roots.

3. Supernumeraries were smaller than basic chromosomes and they did not appear to be heterochromatic. When present in even numbers they paired with themselves. They did not pair with normal chromosomes. In diploid and tetraploid crested wheatgrass transmission of supernumeraries through the egg occurred in haploid numbers. In the pollen directed non-disjunction towards the gametophyte took place with a frequency of approximately 70 per cent. The degree of transmission depended on the numbers of supernumeraries involved and on the genotypes of the parents. Elimination of supernumeraries was generally low but became more pronounced with an increase in their numbers.

Studies concerning the agronomic significance of supernumerary chromosomes allowed the following conclusions:

1. Fertility, plant weight, and plant height were not significantly affected by supernumerary chromosomes in diploid progenies of controlled crosses. A trend towards reduced fertility and yield and increased height was apparent.

2. Tetraploid progenies of controlled crosses showed significantly lower fertility in plants with uneven number of supernumeraries. Plant height was not affected by supernumeraries.

3. Fertility of tetraploid selections with supernumeraries was considerably lower than that of plants without supernumeraries. The main source of fertility variance, however, was genetic. Seed yields in open-pollination progenies of plants with the normal chromosome complement were higher than those in progenies of plants with supernumeraries. In most instances differences in fertility and seed yield were not statistically significant. Forage yield and height in open-pollination progenies did not indicate differential combining ability of parents in the various chromosome groups. Nevertheless, it is concluded that selection against supernumeraries would be beneficial.

This study provided information concerning the cytology of supernumerary chromosomes in crested wheatgrass. The main value of the results in this thesis lies in its application to breeding programs.

PUBLICATIONS

1. Goplen, B. P., J. E. R. Greenshields, and H. Baenziger. The inheritance of coumarin in sweet clover. Can. J. Botany 35: 583-593, 1957.

2. Baenziger, H. and J. E. R. Greenshields. The effect of interspecific hybridization on certain genetic ratios in sweet clover. Can. J. Botany, 36: 411-420, 1958.

BIOGRAPHICAL

1927 —Born in Rebstein, Switzerland.

1947 —Entered Institute of Technology, Zurich, Switzerland.

1951 —Immigrated to Canada.

1954-1958—Student Assistant, Dominion Forage Crops Laboratory, Saskatoon, Saskatchewan.

1957 —M.Sc. in Plant Breeding and Genetics, University of Saskatchewan, Saskatoon, Saskatchewan.

1958 —Research Officer, Forage Crops, Experimental Farm, Lacombe, Alberta.

SUPERNUMERARY CHROMOSOMES IN CRESTED WHEATGRASS

THEIR CYTOLOGICAL BEHAVIOR

AND

BREEDING SIGNIFICANCE

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN THE DEPARTMENT OF FIELD HUSBANDRY
UNIVERSITY OF SASKATCHEWAN

by
Hans Baenziger

Saskatoon, Saskatchewan
March, 1961

TABLE OF CONTENTS

INTRODUCTION

Variations in chromosome number occur between and within individuals of many plant and animal species. In many cases differences are due to varying numbers of supernumerary, accessory, or B-type chromosomes. Supernumerary chromosomes are usually smaller than chromosomes of the basic set. They do not pair with chromosomes of the basic set and in many species they are reported to be heterochromatic. Some species have supernumeraries in somatic and reproductive tissues while others exhibit them only in reproductive tissues. The mode of transmission of supernumerary chromosomes varies in different species. Usually there is directed non-disjunction of the supernumeraries towards the gamete in pollen mitosis. In rye, however, there is directed non-disjunction of supernumeraries in both embryos and pollen grains. In some species directed non-disjunction is not observed.

The origin of supernumerary chromosomes as well as their function remain to be elucidated in most species. It is believed that supernumeraries are genetically modified fragments of normal chromosomes. Some indications of a detrimental effect from supernumeraries have been obtained. Generally, however, they appear genetically inert.

An examination of meiosis in crested wheatgrass (42) indicated a fairly high frequency of supernumeraries in plants of the tetraploid type. Summit and Nordan, varieties of the tetraploid type, and Fairway, a variety of diploid form, are used extensively as forage and seed crops in the drier parts of Western Canada. Extensive breeding programs, designed to

improve both diploid and tetraploid forms of crested wheatgrass, are being conducted at the Forage Crops Section, Canada Department of Agriculture, Research Station, Saskatoon. Since supernumerary chromosomes occur with a high frequency in the Summit variety, and because this variety is characterized by low fertility, this study was initiated to determine the significance of supernumeraries in breeding of improved strains of crested wheatgrass. Investigations of the effect of supernumeraries on fertility were emphasized in particular. Combining ability of selected parents as shown by forage and seed yields of their progenies, was studied in relation to supernumeraries. In addition the present study was designed to investigate more fully the occurrence of supernumerary chromosomes in diploid and tetraploid species of crested wheatgrass and to determine their cytological behavior.

LITERATURE REVIEW

Frequency and Cytological Behavior of Supernumerary Chromosomes

Supernumerary chromosomes occur most commonly in species of the Gramineae. Longley (46) in 1927 reported plants with one to several supernumerary or B-chromosomes in corn (2n=20). Subsequently Randolph (79) observed supernumeraries in 14 of 33 varieties with a plant frequency of 14.3 percent. Some plants contained 8 to 12 B-chromosomes. Supernumeraries were smaller than normal chromosomes and showed irregular behavior during meiosis. Univalent supernumeraries moved undivided to the poles during anaphase I. Non-disjunction of supernumeraries occurred at anaphase II with a frequency of 0 to 100 percent in microspore mother cells and with a frequency of 26 percent in megaspore mother cells. Longley (46, 47) demonstrated that small B-chromosomes originated from large types through exchanges and deletions.

Several authors (16, 19, 79) noted the heterochromatic nature of B-chromosomes in corn. Randolph (79) further noted that B-chromosomes were transmitted freely by male and female gametes, and that as a result of non-disjunction at anaphase II some progeny plants occurred with larger numbers of supernumeraries than expected from parent combinations. In plants with large numbers of B-chromosomes their frequency varied between cells while in plants with low numbers they occurred in constant numbers. Both somatic and reproductive tissues contained supernumeraries.

Roman (81, 82, 83) studied the non-disjunction mechanism in cultures of corn with interchanges between A- and B-chromosomes. Non-disjunction occurred in the majority of microspores in the divisions of the generative nuclei. Crosses involving the A-B interchanges showed that only the translocation chromosomes bearing the B-centromere exhibited non-disjunction. Normal disjunction of supernumeraries was observed in the female. Studies by Blackwood (4) confirmed the findings of Roman. He further noted that a greater proportion of plants in progenies contained even numbers of B-Chromosomes.

Darlington and Thomas (18) and Janaki-Ammal (40) reported B-chromosomes in Sorghum purpureo-sericeum (2n = 10). Plants with supernumeraries occurred in natural populations with a frequency of about 14 percent. The supernumeraries were heterochromatic. They paired with themselves but not with chromosomes of the basic set. In contrast to corn the B-chromosomes of Sorghum were eliminated from most vegetative tissues. In filaments and glumes, however, numerous micronuclei were present. The authors attributed the elimination of the B-chromosomes from most vegetative tissues to an inadequate spindle mechanism. They concluded however that the spindle mechanism functioned normally in cells of the germ track. Directed non-disjunction of B-chromosomes towards the generative nuclei occurred at the second pollen grain divisions. Often the second division was followed by a number of successive divisions (polymitoses). Thus

pollen grains with more than two generative nuclei were formed and these aborted. Darlington and Thomas (18) suggested that these additional cell divisions were stimulated by B-chromosomes.

Fragment chromosomes in addition to the basic complement were observed in rye (2n=14) by Müntzing and Prakken (71) in 1941 and by Müntzing (54). In later reports Müntzing and other Swedish workers adopted the term "accessory chromosomes" to designate these fragments. The most common of these fragments was termed "standard fragment". It was characterized by a subterminal centromere. Other fragment types were presumed to have arisen from the standard fragment by misdivision (60). The largest of the fragment chromosomes was assumed to be an iso-chromosome of the long arm of the standard fragment and it was comparable in size to the smallest of the A-chromosomes.

No pairing of fragments with A-chromosomes was observed. The fragments contained large blocks of heterochromatin. Müntzing (55, 56) and Müntzing and Lima-de-Faria (69) observed that the loss of small fragments during pollen mother cell meiosis was greater than the loss of large fragments. In addition the former were distributed at random in pollen mitosis while the latter showed non-disjunction.

Irregular meiosis was observed in embryo-sacs of plants with large numbers of accessory chromosomes by Håkansson (31). In contrast to corn and Sorghum, non-disjunction of accessories in rye was observed in embryo-sacs as well as in microspore mother cells. Plants with 15 to 20

accessories showed supernumerary nuclei in the embryo-sacs and these plants were sterile.

Müntzing (59) observed a grouping of accessories according to size in somatic metaphase plates. The smallest fragments assumed the most central positions. Detailed pachytene analyses by Müntzing and Lima-de-Faria (67, 68) confirmed that the standard fragment had given rise to other fragment types. Thus the small fragment corresponded to the short arm of the standard fragment. The medium size fragment was an iso-chromosome of the small fragment and the large fragment represented an iso-chromosome of the long arm of the standard fragment.

Håkansson (35, 36) studied meiosis and pollen mitosis in rye plants with four to eight accessory chromosomes. In some instances good pairing between accessories occurred while in others univalents were most common. Some trivalent associations of accessories were observed. Irregularities in meiosis I were common. Univalents were lagging and some divided at anaphase I. Occassionally restitution nuclei were formed after anaphase I and in some cases three telophase nuclei were formed. Meiosis II showed fewer irregularities. Disturbed pollen mitoses were most frequent in plants with large numbers of accessories.

Surveys of rye populations from the Middle East and Asia (62, 64) showed accessories to be present in varying frequencies. These accessories were of the same morphological

type as the standard fragment in Swedish material. These surveys also revealed a preponderance of plants with even numbers of accessories.

Sarvella (86) observed a great variety of morphological types of accessory chromosomes in tetraploid rye. Pairing between accessories was poorer than in diploids. Plants with odd numbers of accessory chromosomes were as common as plants with even numbers. The author suggested that natural selection against gametes carrying accessories occurred in tetraploid populations.

Accessory chromosomes have been reported in several species of the genus Poa. Müntzing (57, 58, 70), Håkansson (32, 34) and Milinkovic (52) studied various populations of P. alpina (2n=14). Accessories were present at meiosis in most of these populations but they were absent in adventitious roots. Some exceptions were noted by Müntzing (70). Accessory chromosomes in P. alpina were smaller than normal chromosomes, they appeared to be heterochromatic and they showed good pairing with themselves but not with A-chromosomes. They were generally transmitted through the male and female in haploid numbers. Milinkovic (52) observed that in plants with accessories at meiosis, primary roots and stem tissue also contained accessory chromosomes. The author suggested that elimination of accessories from adventitious roots occurred at a very early stage of development, probably in the first divisions of the pericycle layer.

Nygren (74) observed accessory chromosomes in P. timoleontis (2n=14). Their cytological behavior was similar to that of accessories in P. alpina. In P. trivialis (2n=14) Bosemark (12) observed that 11.5 percent of the plants contained accessory chromosomes and they were present in somatic and reproductive tissues.

Bosemark (6, 7, 9) described accessory chromosomes in Festuca pratensis (2n=14) and F. arundinaceae (2n=42). In wild populations of F. pratensis 24.6 percent of the plants contained accessories. In F. arundinaceae 54.5 percent of the plants contained accessories. As in rye, four types of accessories were distinguished according to size. It was believed that the small types had arisen through fragmentation of larger accessories. Somatic and reproductive tissue of these species contained accessory chromosomes and these appeared to be heterochromatic. In somatic plates these chromosomes assumed a central position. F. pratensis plants with accessory chromosomes showed a high univalent frequency. Univalents usually lagged in the meiotic divisions but elimination, as indicated by the presence of micronuclei in pollen quartets occurred in less than 50 percent of the pollen mother cells. Accessories showed 5 to 90 percent non-disjunction at the first pollen mitosis. The genetic constitution of the plants involved appeared to be the main cause of variation in the frequency of non-disjunction. In the female the accessories were distributed at random. The smallest accessory chromosome showed directed

non-disjunction at pollen mitosis only in the presence of larger types of accessories.

In natural populations of Phleum phleoides (2n=14) and P. nodosum (2n=14) plants with accessory chromosomes were observed with frequencies of 31.1 percent and 12.5 percent respectively (5, 10, 12). These species as well as Briza media (2n=14), Holcus lanatus (2n=14) and Alopecurus pratensis (2n=28) contained accessories in somatic and reproductive tissue (12). Haploid transmission of accessories occurred in P. phleoides while in the other species directed non-disjunction towards themale gamete was general.

Chennaveeraiah and Love (14) reported supernumerary chromosomes in root tips of Aegilops columnaris (2n=28) and A. cylindrica (2n=28). The authors suggested that they had arisen by misdivision of normal chromosomes. It was thought possible however that chromosome fragmentation had occurred as a result of the root treatment with hydroxyquinoline. Markarian and Schultz-Schaeffer (50) stated that cytological manipulation caused chromosome breakage in their material and gave rise to supernumerary fragments.

Several authors (29, 84, 85, 90, 91, 95) observed supernumerary chromosomes in non-graminaceous species of monocotyledons. In Allium cernuum (2n=14) B-chromosomes were generally unpaired while in Lilium medeoloides (2n=24) they paired with themselves but not with A-chromosomes. In dicotyledons, species with supernumerary chromosomes are not as

common. Some plants of Clarkia elegans (2n=18) contained supernumeraries which were indistinguishable from A-chromosomes (43, 44, 65). They had no phenotypic effect and it was concluded therefore that these plants were not true aneuploids. Diverse populations of Centaurea scabiosa (2n=20) contained accessories in varying frequencies (23, 24, 25). They were present in vegetative and reproductive tissues and they were smaller than A-chromosomes. In this species the assessories were generally transmitted in haploid numers through male and female but in some instances considerable elimination occurred at meiosis. These chromosomes were maintained at a constant level in many populations and it was concluded that natural selection favored plants with accessories.

Berger et al. (1, 2, 3) and Witkus et al. (94) observed supernumerary chromosomes in Xanthisma texanum (2n=8). In this species they were present at meiosis and in stem tissue but not in root tips.

Several authors (21, 27, 28, 33) studied B-type chromosomes in Achillea asplenifolia (2n=18), Godetia vimenea (2n=18), several species of Crepis and Plantago serraria (2n=10). In some of these populations the additional chromosomes could not be distinguished from A-chromosomes while in others they were heterochromatic. They had no phenotypic effects. The accessories in P. serraria differed from any reported previously in that they displayed directed non-disjunction towards the egg.

Various animal species, particularly insects, have been found to possess supernumerary chromosomes (51, 80, 93). In some species these chromosomes were heterochromatic and showed

non-disjunction at meiosis. In others, supernumeraries were associated with sex-chromosomes (39, 51), and appeared the result of disturbed sex-determining mechanisms.

Agronomic Significance of Supernumerary Chromosomes

Previous studies of supernumerary chromosomes have emphasized their morphology and cytological behavior as well as their frequency in various populations. Few studies have been specifically designed to assess their agronomic significance. Östergren (75) stated however that accessory chromosomes have no useful function and "that they often lead an exclusively parasitic existence".

Pollen viability was not adversely affected by B-chromosomes in corn (46). Embryo-sac mother cells suffered a higher death rate in the presence of B-chromosomes. Genetic tests by Randolph (79) involving genes located on 17 arms of the basic chromosome complement revealed that these chromosome regions were not represented in the B-chromosomes. Reduced fertility and vigor of corn plants with more than ten B-chromosomes was noted (79, 92). Reproduction failed entirely if the number of B-chromosomes exceeded 20. Catcheside (13) observed preferential fertilization by male gametes with B-chromosomes.

Müntzing (53, 63) reported significant negative correlations between the number of accessories and kernel weight, number of kernels per ear, percent seed set and pollen fertility

in rye. Vegetative development also was adversely affected. Cell size was significantly increased in rye plants with two standard fragments (66) and pollen development was retarded (61).

Festuca pratensis populations from diverse soil-climatic regions showed different frequencies of accessory chromosomes and Bosemark (8, 11) concluded that these chromosomes affected plant adaptability. In plants with large numbers of accessories pollen fertility was significantly reduced. Reduction in seed set appeared more pronounced than reduction in pollen stainability and the author concluded that stainability did not indicate the capacity of pollen to function. Although significant negative correlations between the number of accessories and forage yield were obtained in some cases, Bosemark (11) stated that "the deleterious effects of even the highest numbers of accessory chromosomes on the vegetative development must be considered relatively moderate". In Anthoxanthum pollen mitosis was irregular and fertility was depressed in plants with one to four accessories (45, 76).

Accessory chromosomes in Centaurea scabiosa were responsible for a reduction in fertility and vegetative development (22, 26). In most cases these negative effects were non-significant. Plants of Plantago coronapus having an entirely heterochromatic B-chromosome were male sterile while plants lacking this chromosome were male fertile.(77).

Several authors (38, 73, 87, 88) noted considerable variation in the somatic and meiotic chromosome numbers of

Bromus inermis. Some considered chromosomes in addition to the basic complement of the species analogous to inert B-chromosomes (38, 73). Fertility was reduced in brome plants with chromosome numbers higher or lower than 56 and in plants showing meiotic irregularities (87, 88).

Cytological Studies in the Genus Agropyron

The assignment of the various morphological forms within the genus Agropyron to taxonomic units is inconsistent, therefore the species designations used by the various authors are not comparable in all instances.

Peto (78) reported 2n chromosome numbers of 14 and 28 for A. cristatum, of 28 for A. desertorum and of 14 to 17 for A. spicatum. One plant of A. cristatum had 29 chromosomes and three plants of A. spicatum had one to three additional chromosomes. Meyers and Hill (72) observed 28 chromosomes in their material. One plant had 31 chromosomes. Hartung (37) noted that aneuploid counts were obtained very rarely in Agropyron. He reported chromosome numbers of 28 for A. sibiricum and A. michnoi. In A. cristatum he noted 14 and 28 chromosome forms.

Hair (30) described a dicentric chromosome in plants of A. scabrum with 41 chromosomes. The dicentric was unstable and subsequently gave rise to smaller monocentrics.

Knowles (42) described six morphological forms of crested wheatgrass and assigned them to the species A. cristatum,

A. desertorum, A. sibiricum, A. michnoi, A. imbricatum and A. fragile. In nine strains of A. cristatum somatic counts of 2n=14 were obtained. Two additional strains of this species had 28 chromosomes. The remaining species were tetraploids with somatic chromosome numbers of 28. One plant of A. desertorum had 29 chromosomes and one plant of A. michnoi was found to be triploid.

At the first meiotic metaphase in pollen mother cells considerable variation in chromosome numbers were noted. Fourteen of 43 tetraploid plants belonging to the strain S-841 of A. imbricatum and to A. desertorum and A. michnoi were found to have one to six supernumeraries. All plants of A. sibiricum and A. fragile possessed the normal tetraploid chromosome complement, while all plants of the Fairway strain of A. cristatum had the diploid complement of 14 chromosomes.

Preliminary observations by Knowles (42) did not indicate any relationship between the occurrence of supernumeraries and plant vigor. Supernumerary chromosomes were smaller than normal chromosomes in some plants but in others they could not be distinguished. They did not show a differential staining reaction. Since no supernumeraries were observed in diploid crested wheatgrass the author suggested that their origin and maintenance were related to the more complex pairing relationships in tetraploids. Several crosses indicated that supernumerary chromosomes in crested wheatgrass were transmitted through pollen and eggs.

MATERIALS AND METHODS

Plant Materials

Several of the strains used were previously described by Knowles (42). They represented the three species Agropyron cristatum (L.) Gaertn., A. desertorum (Fisch.) Schult. and A. imbricatum (M.B.) Roem. and Schult.

The diploid species, A. cristatum was represented by the Fairway variety, strain S-3541 from Sweden and strain S-5239 from the Soviet Union. A survey of meiotic chromosome numbers was conducted in these three populations. Selected plants of S-3541 were used for studies of mitosis. Transmission of supernumerary chromosomes was investigated using controlled crosses. Controlled crosses were made by the interpollination of plants without emasculation. Emasculation was omitted in view of the high degree of self-sterility shown by crested wheatgrass.

Several tetraploid populations were used. They included the varieties Nordan and Summit (S-131), the strains S-1333 and S-841, and a group of selections made in the breeder's seed plot of Summit and a foundation field of Summit. S-841 belongs to the species A. imbricatum, while the remaining populations belong to A. desertorum. Since A. imbricatum resembles A. desertorum and is highly compatible with it (42), independent classification may not be required. These populations were used for a survey of meiotic chromosome numbers. Progenies of

controlled crosses between plants of S-841 and S-1333 were involved in a study of the transmission of supernumerary chromosomes in tetraploid crested wheatgrass. The agronomic significance of supernumeraries was evaluated in diploid and tetraploid progenies of controlled crosses, in selected plants of S-841, S-1333, and Summit, and in open-pollination progenies of the selections.

The Summit selections were collected prior to seed harvest. The main objective in selection was high fertility combined with agronomic desirability. The average fertility of 36 selections from the [illegible] breeders plot was 56 percent as compared to 38 percent for the entire plot. The average fertility of 23 selections from the foundation field was 56 percent as compared to 44 percent for the entire field.

Cytological Methods

Chromosome counts were obtained from temporary smear preparations. Root tips and stem tissue were fixed in a 3:1 alcohol-acetic-acid mixture following pretreatment for one-half to one hour in paradichlorobenzene. Spikes used for the study of pollen mother cell meiosis were fixed in a 6:3:1 solution of 95 percent ethyl alcohol, chloroform, and acetic-acid. All preparations were stained with acetocarmine. Meiotic chromosome counts were based on eight to ten cells per plant in most cases. These were usually obtained from one or two spikes. In this report total chromosome numbers, 14, 15, 16 etc. and 28, 29,

30 etc. are presented, and include the chromosomes of the basic complement plus supernumeraries. Thus a count of 15 refers to 14 basic chromosomes and one supernumerary. Similarly a count of 29 refers to 28 basic chromosomes and one supernumerary.

Material for cytological studies was collected from plants in the field and in the greenhouse. Primary roots were obtained from seeds germinated in vermiculite. Metaphase and diakinesis stages were used for meiotic chromosome counts. Anaphase stages were usually avoided because univalents occasionally divide at anaphase I. In tetraploid material the quadrivalent frequency was recorded. Since variation in quadrivalent frequency between cells within plants appeared as large as variation between plants it is not reported in detail. Generally one to three quadrivalents per cell were noted.

In diploid crested wheatgrass the study of the transmission of supernumeraries involved 188 plants representing progenies of 21 crosses. In most cases reciprocal crosses were studied. Parents with zero, two and four supernumeraries were involved. The number of plants examined varied from six to twelve per cross and ten or more cells were counted for each plant.

A similar study in tetraploid material included progenies of seven crosses. Parents with zero, two and five supernumeraries were involved. A total of 68 progeny plants were examined. The average number of cells counted per plant was slightly below

ten because of difficulties in obtaining good preparations.

Some variation in chromosome numbers between cells within plants occurred. Therefore the mean number of supernumeraries was calculated for each progeny on a per cell basis.

Description of Field Tests

Observations concerning the agronomic significance of supernumerary chromosomes were made in spaced-plant plantings. Fertility, height, forage yield, and seed yield were studied. In 1958 and 1959 observations were made on fertility, plant height, and plant weight in the progenies of the controlled crosses among plants of S-3541, which strain was used for the study of the transmission of supernumeraries. In 1960, fertility and height were measured in the tetraploid progenies of controlled crosses. These populations were grown in single progeny rows without replication, thus no measure of environmental influence could be obtained.

Data on fertility, seed yield, forage yield, and height were obtained in three tests of open-pollination progenies. These tests will be referred to as tests 1, 2 and 3 respectively. Tests 1 and 2 each included 64 strains arranged in an 8 x 8 partially balanced lattice design with three replications. These two tests were established in 1957 and 1958 respectively and they included progenies of selected parents belonging to the strains S-841 and S-1333. In addition the check varieties Summit and Nordan and some miscellaneous materials were included.

Test 3, established in 1959, included open-pollination progenies of the Summit selections and the varieties Summit and Nordan. The 36 entries were arranged in a 6 x 6 lattice design using three replications. In these three tests, plots consisted of 11 plants spaced 2' apart in single rows, spaced 3' apart.

Fertility data from test 1 were obtained in 1958 and 1959, Forage yields, seed yields, and heights are reported for 1959. In test 2 fertility, heights, and seed yields were recorded in 1959 and forage yields in 1959 and 1960. All observations in test 3 were made in 1960. In order to obtain forage yields and seed yields simultaneously the tests were cut just prior to seed maturity.

The parents of tests 1 and 2 were evaluated for fertility in a polycross which will be referred to as test 4. These parents were represented by one clone* in each of the five replicates. Clones were spaced 2' x 3'. The parents of test 3 were evaluated in an isolated polycross block with three replications. Each selection appeared once in each replicate and clones were spaced 4' x 4'. This test will be referred to as test 5.

Method of Rating Fertility

Fertility ratings were based on observations from two mature spikes per plant. From each spike, five or ten spikelets were selected avoiding the bottom and top spikelets. By pressing on the individual florets with a sharp pencil the number of fully developed seeds was determined. Subsequently

*In this thesis the term "clone" refers to individual, vegetatively reproduced plants of selections.

a fertility value in percent was calculated for each spikelet. The individual spikelet values were averaged to obtain the spike fertility and the two spike values were averaged to obtain the fertility rating for individual plants or clones.

In the progenies of the controlled crosses and in test 4 ten spikelets per spike were used. In test 5 and in the tests of open-pollination progenies five spikelets per spike were counted. The fertility values of parents in test 4 represented the means of five clones. Assuming an average of five florets per spikelet each parent value was thus based on 500 individual observations. Similarly fertility ratings of the parents in test 5 were based on 150 observations. In all open-pollination progenies, five plants were sampled in each of the three replicates. Progeny fertility values used in the subsequent analyses thus represented the means of 15 individual plant ratings. Assuming fiwe florets per spikelet progeny fertility percentages were therefore based on 750 individual observations.

Expressing fertility as the total number of seeds in percent of the total number of florets examined in each parent or strain (maximum likelihood method) would have given the lowest estimate of fertility variance. However this method was not used. Instead fertility indices in percent were calculated for spikelets and spikes, and these were averaged for clones and progenies. This method was preferred because it made the calculation of variance components possible.

Statistical Methods

It was intended to relate fertility of open-pollination progenies to fertility of their parents and to the chromosome number of their parents. Progenies in tests 1, 2, and 3 were classified according to parental strains, that is S-841, S-1333, and Summit selections. Progenies within strains were assigned to groups according to the chromosome number of the female parent and the mean fertilities of groups were calculated. The analysis of variance was performed using spike fertility values as the smallest unit. The following variance components were then computed;

1. Variance between spikes within plants (error).
2. Variance between progeny plants within female parents.
3. Variance between female parents within parental chromosome groups.
4. Variance between chromosome groups.

Degrees of freedom, sums of squares, and expectations of mean squares for these components were calculated as indicated in Table 1.

Table 1. Analysis of variance used in deriving variance components.

Variance	Degrees of Freedom*	Sums of Squares**	Components of Variance***
Total	$n - 1$	A-E	$\sigma^2+k_3\sigma^2_{pr}+r_2\sigma^2_{par.}+s_1\sigma^2_{gr}$
Chromosome groups	$n_g - 1$	D-E	$\sigma^2+k_2\sigma^2_{pr}+r_1\sigma^2_{par.}+s\sigma^2_{g}$
Parents within groups	$(n_{p1}-1+\ldots +(n_{pn}-1)$	C-D	$\sigma^2+k_1\sigma^2_{pr}+r\sigma^2_{par.}$
Progeny plants within parents and groups	$n_p(n_{pr}-1)$	B-C	$\sigma^2+k\sigma^2_{pr}$
Spikes within plants	$\frac{n}{2}$	A-B	σ^2

*n = total number of spikes
n_g = number of chromosome groups
n_p = total number of progenies
$n_{p1}\ldots n_{pn}$ = number of progenies in first to nth group
n_{pr} = number of individual plants per progeny

** A = Total
B = Spikes
C = Parents
D = Groups
E = Correction fact

*** Expectations of the mean squares were obtained in the manner described by Kempthorne (41) and Comstock and Robinson (15).

Tests of significance were conducted according to the proeedures outlined for hierarchial classifications (41). F-values were therefore calculated as follows:

F_i for differences between progeny plants $= \frac{\sigma^2+k\sigma^2_{pr}}{\sigma^2}$

F_{ii} for differences between parents within groups $= \frac{\sigma^2+k_1\sigma^2_{pr}+r\sigma^2_{par}}{\sigma^2+k\sigma^2_{pr}}$

F_{iii} for differences between groups $= \frac{\sigma^2+k_2\sigma^2_{pr}+r_1\sigma^2_{par}+s\sigma^2_{gr}}{\sigma^2+k_1\sigma^2_{pr}+r\sigma^2_{par}}$

The parent fertility data were analysed in the same manner considering the following variance components: Spikes within clones, clones within parents, parents within groups, and chromosome groups.

Since the fertility data were expressed as percentages all subsequent calculations were made using the values transformed to $\sin^2 \theta$. Several analyses were performed on both the percentage data and the transformed values to determine the effect of the transformations on the results.

Forage yield, seed yield, and height were measured on a plot basis for all entries in progeny tests 1, 2, and 3. In the analyses of forage yield and seed yield data the effects of missing plants were determined by co-variance methods. If the regression of yield on number of plants per plot was significant the appropriate corrections were made and the data were analysed by the randomized block method. If this regression was not significant the lattice analysis was performed. The progenies were then grouped according to the parental chromosome numbers and comparisons were made between groups by means of t-tests.

Heritability estimates for fertility were obtained by doubling open-pollination progeny-parent regressions. Regression techniques also were employed to establish the relationship between fertility and seed yield.

RESULTS

Cytological Studies

The occurrence of supernumerary chromosomes in various plant parts

Among 24 plants belonging to S-3541, 23 were found to have one to four supernumeraries at pollen mother cell meiosis. The seven bivalents of the basic complement were of equal size. Generally five to seven of these showed chiasmata on both sides of the centromere while zero to two were rod bivalents. The supernumeraries appeared as small rod bivalents or univalents.

Adventitious roots were examined for 20 of these plants and in all cells counted there were 14 chromosomes. Open-pollinated seed from a plant having two supernumerary bivalents was germinated and subsequently primary roots were examined. A total of 16 cells was counted with most of these coming from different roots. One cell had 14 chromosomes and the remainder had 15 to 18. For the 18 chromosome plant several telophase stages were observed with free chromatin in the cytoplasm.

After removal of primary roots the seedlings were planted in soil and successfully established. At the three to four leaf stage adventitious roots were fixed. From these, ten cells representing three plants were counted and all contained 14 chromosomes. Stem meristem from an additional plant was studied and eight cells contained 16 or more chromosomes.

In some of the cells from primary roots and stem tissue the supernumeraries could be clearly distinguished. They were short with subterminal centromeres. However the supernumeraries

did not differ from normal chromosomes in their stainability. Similarly the supernumeraries in the pollen mother cells did not appear to be heterochromatic.

Frequency of supernumerary chromosomes in various populations

a. Diploid populations

Twenty-five plants of the Fairway variety, grown from breeders seed were examined. A total of 260 cells including 69 diakinesis stages, 171 metaphase plates, and 20 anaphase groups were counted. In all of these, seven bivalents were observed (Fig. 1), and distributions were 7 + 7 in the anaphases.

The frequency of plants in S-3541 with various meiotic chromosome numbers is presented in Table 2.

Table 2: Frequency of plants with various meiotic chromosome numbers in S-3541 crested wheatgrass.

Percent Plants with Chromosome Numbers of					No. of Plants Examined	Total No. Cells Counted
14	15	16	17	18		
4.2	8.3	66.7	8.3	12.5	24	118

The majority of the plants contained supernumeraries and even numbers were more common than uneven numbers. Three plants of S-5239 were studied and these had one, two, and four supernumeraries at meiosis.

Plate I

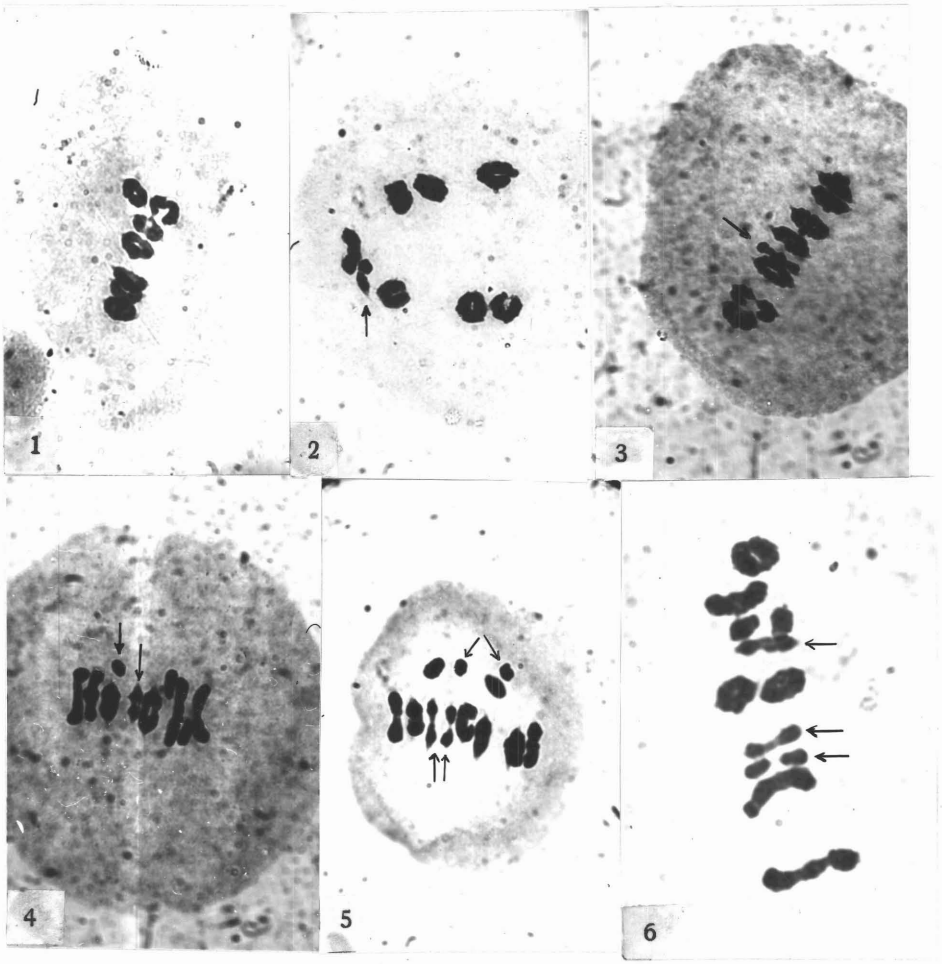

Fig. 1-6. Meiosis in pollen mother cells of diploid crested wheatgrass. (Arrows indicate supernumerary chromosomes, magnification approximately 750X.)

Fig. 1. Metaphase I, Fairway, 7 II

Fig. 2, 3. Metaphase I, S-3541, 8 II

Fig. 4. Metaphase I, S-3541, 7 II + 3 I

Fig. 5. Metaphase I, S-3541, 8 II + 4 I

Fig. 6. Metaphase I, S-3541, 9 II + 2 I

Plate II

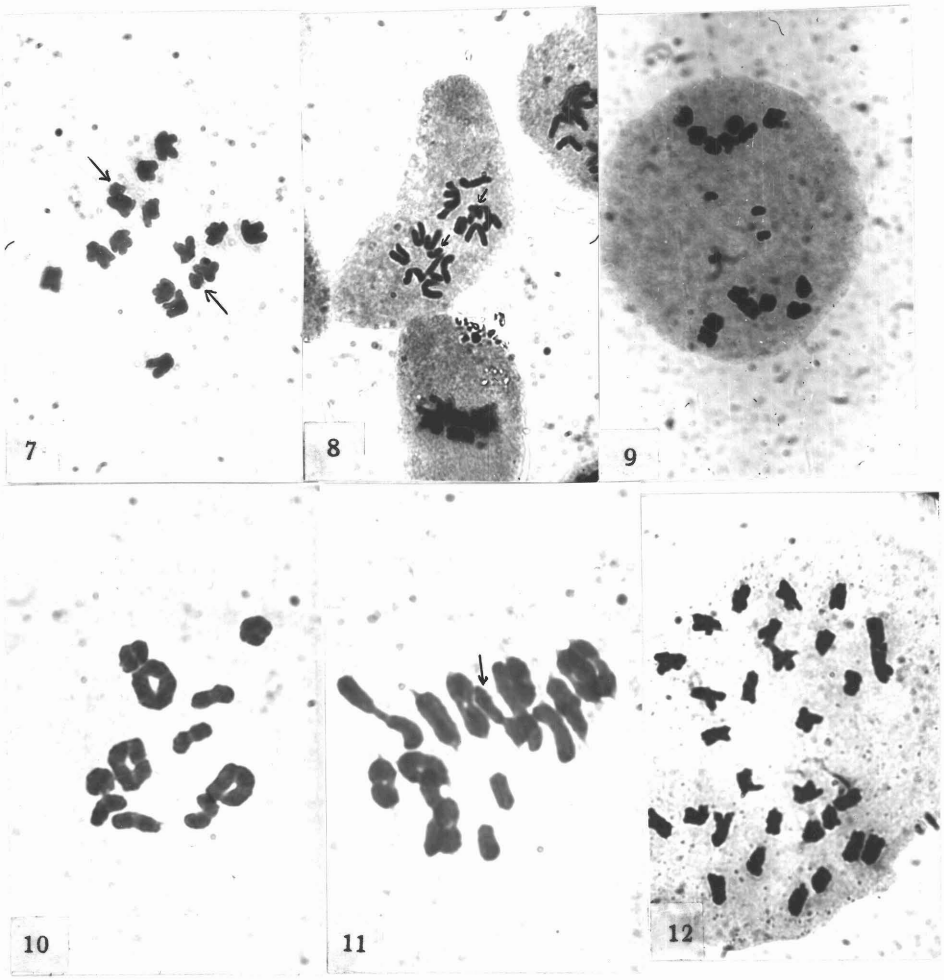

Fig. 7-9. Meiosis in pollen mother cells of diploid crested wheatgrass.

Fig. 7. Anaphase I, S-3541, 8 + 8
Fig. 8. Anaphase II, S-3541, 8 + 8
Fig. 9. Anaphase I, S-3541, 7 + 7 + 2, precocious divisions of 2 supernumerary univalents.

Fig. 10-12 Meiosis in pollen mother cells of tetraploid crested wheatgrass.

Fig. 10. Diakinesis, Nordan, 3 IV + 8 II
Fig. 11. Metaphase I, Nordan, 14 II + 2 I
Fig. 12. Anaphase I, Nordan, 15 + 15

Plate III

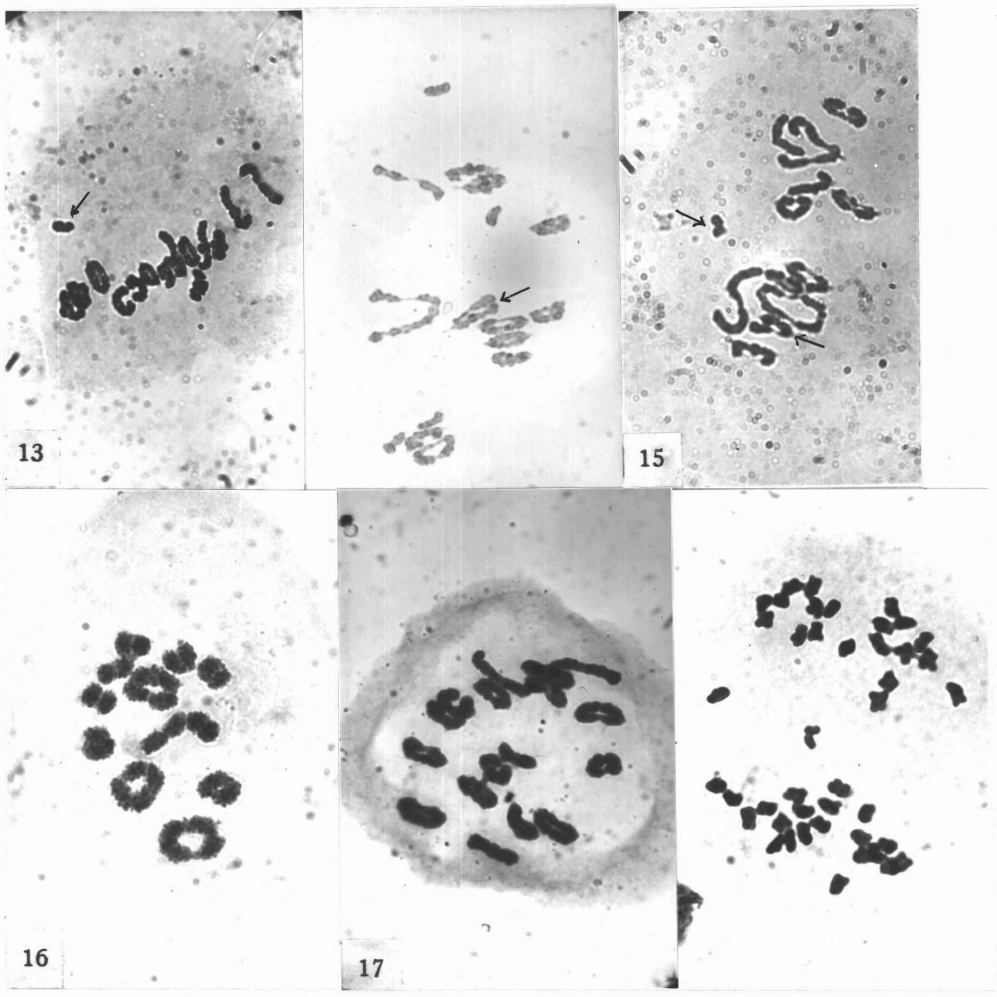

Fig. 13-18. Meiosis in pollen mother cells of tetraploid crested wheatgrass.

Fig. 13. Metaphase I, Nordan, 1 IV + 12 II + 1 I

Fig. 14. Metaphase I, Summit, 1 IV + 1 III + 11 II + 2 I

Fig. 15. Metaphase I, S-841, 3 IV + 1 III + 8 II + 1I

Fig. 16. Diakinesis, S-841 x S-1333, 3 IV + 9 II

Fig. 17. Metaphase I, S-841 x S-1333, 2 IV + 13 II

Fig. 18. Anaphase I, S-841 x S-1333, hexaploid, approximately 21 + 21

b. Tetraploid populations

The results of a survey of meiotic chromosome numbers in five populations are included in Table 3.

Table 3: Frequency of plants with supernumerary chromosomes at meiosis for five populations of tetraploid crested wheatgrass.

Population	Percent Plants with Chromosome Number of: 28	29	30	31	32	33	No. of Plants Examined	No. of Cells Counted	Av. No. Supernum. per Plant
Nordan	11.5	19.2	53.8	7.7	7.7	-	26	229	1.7
Summit	35.7	14.3	35.7	-	14.3	-	14	116	1.4
S-841	18.0	38.6	27.3	11.4	2.3	2.3	44	376	1.5
S-1333	63.1	15.8	21.1	-	-	-	19	144	.7
Summit selections	29.4	35.3	20.6	8.8	5.9	-	34	308	1.3

Supernumerary chromosomes were most abundant in the Nordan variety where 88.5 percent of the plants contained them (Fig. 10-13). The Summit variety showed a lower frequency of supernumeraries than Nordan. In both populations plants with even numbers of additional chromosomes were more common than plants with uneven numbers. The two experimental strains differed considerably in the frequency of plants with supernumeraries. In S-841, plants with one to five supernumeraries occurred whereas in S-1333 only plants with one and two were noted.

Selection of plants in Summit with high fertility did not materially alter the mean number of supernumeraries. In selected plants 29.4 percent lacked supernumeraries as compared to 35.7 percent in unselected Summit. However, in the selections a larger proportion of the plants had one and a smaller proportion had two additional chromosomes.

Behavior of supernumerary chromosomes at pollen mother cell meiosis

Pairing relationships and the behavior of supernumerary chromosomes at meiosis were essentially the same in diploid and tetraploid forms of crested wheatgrass.

In plants having an even number of supernumeraries they usually appeared at the metaphase plate simultaneously with the chromosomes of the normal complement. Generally they formed bivalents which were one-third to one-half the size of A-bivalents (Fig. 2-6). In cells containing two supernumerary bivalents these were commonly found adjacent to each other near the center of the plate. However they did not appear to be in quadrivalent association. The supernumeraries were never observed in association with chromosomes of the basic set. During anaphase I the supernumeraries moved to the poles simultaneously with the A-chromosomes (Fig. 7). Occasionally they lagged but since dyads with micronuclei were extremely rare it was concluded that the laggards were usually included in the daughter nuclei. During meiosis II the supernumeraries showed normal disjunction and movement to the poles (Fig.8).

Pollen quartets with micronuclei were extremely rare. Thus elimination of supernumeraries during meiosis was low.

Where a single supernumerary chromosome was present it moved to the metaphase plate and subsequently to one of the poles or it remained at one of the poles during the first division. The equational division of the univalent followed at anaphase II. In only one diploid and a few tetraploid plants did supernumerary univalents divide at anaphase I (Fig. 9).

Trivalent associations of supernumeraries were rarely distinguished in cells of diploid plants. In tetraploid material they were more frequent (Fig. 15). In plants having four supernumerary chromosomes these were present as two bivalents in most cells.

Anaphase distributions of 7 + 9 could occasionally be observed on the same slide with 8 + 8 distributions in diploids. Similarly 14 + 16 distributions occurred with 15 + 15 distributions in tetraploids. In the cells with uneven distributions the chromosomes of the basic set were always found in even distributions. Irregular disjunction of supernumeraries may have occurred as a result of stickiness or because of centromere deficiencies.

Transmission of supernumerary chromosomes

a. Diploid populations

This study involved progenies of ten plants in various cross combinations. Three plants had seven pairs of chromosomes

at meiosis, three plants had eight, and four plants had nine. The results from this inheritance study are summarized in Table 4. With the exceptions of crosses 16 and 18, crosses are listed in ascending order according to the mean number of supernumeraries in the progeny.

In crosses 1 - 10 only the female parent had supernumerary chromosomes, with two in the first two crosses and four in the following eight. The progenies of crosses 5 and 8 showed the same chromosome number in all cells of all plants. In the remaining crosses the chromosome number varied between progeny plants and between cells within plants. The majority of the cells, however, contained half the number of supernumeraries of the female parent.

Similar ranges of chromosome numbers also appeared in the progenies of crosses 14 to 19 where the male parent carried supernumeraries and in the progenies of crosses 11 to 13 and 20 to 21 where both parents carried supernumeraries.

For the crosses 14 to 19, which were reciprocals of crosses 3 to 8, 53 progeny plants were examined. Eleven of these had 16 chromosomes. In this portion of the population transmission of supernumeraries through the male occurred in haploid numbers. Of the remaining plants 12 had 18 chromosomes in all cells, 26 showed chromosome numbers ranging from 16 to 20 within individual plants and four plants were without supernumeraries. In the plants with 16 to 20 chromosomes the majority of cells contained 18 chromosomes. In these matings the male

presumably contributed 18 chromosomes and subsequent irregular cell divisions were responsible for the ranges in the chromosome numbers. Thus 38 plants or 71.7 percent showed directed non-disjunction of supernumeraries towards the male gametes.

In crosses 3, 4, 8, and 10 the same male parent, plant I, was involved with different female parents. The mean number of supernumeraries varied from 1.77 in cross 3 to 2.50 in cross 10. In crosses 16 to 18 plant I was used as female parent in combination with different male parents. The mean number of supernumeraries ranged from 2.59 in cross 18 to 3.72 in cross 17. It appeared therefore that the degree of transmission varied according to the genotype of the parents and the resulting zygotes.

In the progenies of crosses 11 to 13 and 20 to 21 the mean numbers of supernumeraries were lower than expected assuming haploid transmission through the female and diploid transmission through the male. This was due to a higher degree of elimination particularly in the crosses where larger numbers of supernumeraries were involved.

The summary shows that in groups 1 and 2 the mean number of supernumeraries was somewhat higher than the haploid number contributed by the female parents. This would indicate a degree of directed non-disjunction of supernumeraries towards the female gametes. This, presumably, also occurred in groups 3 and 5 but because of high elimination the mean numbers of supernumeraries were lower than expected.

Table 4: Transmission of supernumerary chromosomes in crosses of diploid crested wheatgrass.

No. of Cross	Description of Cross: Parents	Description of Cross: Chromosome Number	No. of Progeny Plants	No. of Cells Observed	Mean No. of Supernumeraries in Progeny	No. of Cells with Chromosome No.: 14	15	16	17	18	19	20	21	22
	A. Individual crosses													
1	A x H	16 x 14	10	138	1.00	13	111	14						
2	C x H	16 x 14	12	169	1.29		129	30	10					
3	D x I	18 x 14	9	112	1.77		27	84	1					
4	E x I	18 x 14	10	140	1.98		2	138						
5	E x J	18 x 14	9	98	2.00			98						
6	D x J	18 x 14	10	116	2.00			115	1					
7	G x J	18 x 14	7	121	2.00			120	1					
8	G x I	18 x 14	9	104	2.00			104						
9	F x J	18 x 14	10	112	2.09	30		32	29	21				
10	F x I	18 x 14	9	130	2.50		1	64	63	2				
11	C x B	16 x 16	7	100	2.58		19	4	77					
12	A x B	16 x 16	9	133	2.75			41	85	6	1			
13	B x A	16 x 16	9	131	2.86			20	109	2				
14	J x G	14 x 18	7	111	3.37			30	9	72				
15	J x E	14 x 18	10	130	3.44			36		94				
16	I x D	14 x 18	9	131	3.27	14		19	2	95		1		
17	I x E	14 x 18	10	132	3.72			18		114				
18	I x G	14 x 18	9	111	2.59	34		10		67				
19	J x D	14 x 18	8	101	4.00					101				
20	D x E	18 x 18	9	111	4.94			18		18	15	54	2	4
21	E x D	18 x 18	6	77	5.01			2	6	28	9	19	11	2
	Total		188	2508		91	289	997	393	620	25	74	13	6
	B. Summary of crosses according to parental chromosome numbers													
Group 1		16 x 14	22	307	1.16	13	240	44	10					
Group 2		18 x 14	73	933	2.11	30	30	755	95	23				
Group 3		16 x 16	25	364	2.74		19	65	271	8	1			
Group 4		14 x 18	53	716	3.40	48		113	11	543		1		
Group 5		18 x 18	15	188	4.99			20	6	46	24	73	13	6

b. Tetraploid populations

This study included progenies of five plants which were crossed in various combinations. Two parents had no supernumeraries, two plants had two and one plant had five. Clones of the progeny plants were grown in the greenhouse for observation of meiosis. The results of this study are included in Table 5.

In the first two crosses the same female parent with two supernumeraries was pollinated by different males having the normal chromosome complement. Of the ten progeny plants of cross 1 four were free of supernumeraries and six plants had one supernumerary. In cross 2 all but one of the plants had one additional chromosome. One hybrid plant had 42 chromosomes (Fig. 18). This plant was assumed to be a hexaploid resulting from the union of an unreduced gamete with one containing the haploid chromosome complement. The mean number of supernumeraries for crosses 1 and 2 were .48 and 1.00 respectively. Since the number of plants studied was relatively small this difference may be due to chance. However, a difference of about the same magnitude occurred between the reciprocal crosses 3 and 4. It appears more probable therefore, that in the hybrids of plants A and B the supernumeraries were eliminated after the zygotes were formed and that differences in genotypes of plants B and C were responsible for differential elimination.

In cross 3 four plants had no supernumeraries, one plant had one, and five plants had two. Cross 4 produced one plant without supernumeraries, seven plants with two, and two plants

with three. As was noted in the reciprocal crosses elimination was higher in the B x A cross than in the C x A combination. The total of crosses 3 and 4 indicated that complete elimination of supernumerary chromosomes in the male occurred in five plants or 25 percent of the population. Haploid transmission through the male occurred in five percent of the matings and directed non-disjunction of supernumeraries towards the male gamete took place at a frequency of 70 percent. Two progeny plants of cross 4 contained 31 chromosomes. Presumably they were produced by the combination of normal eggs with 16 chromosome pollen followed by non-random distribution of the supernumeraries, or by matings between normal eggs and pollen with more than 16 chromosomes. Such pollen could be produced by uneven distribution of supernumeraries during meiosis in the male parent followed by directed non-disjunction at pollen mitosis.

Seven plants in cross 5 possessed three supernumeraries in all pollen mother cells. According to observations in crosses 1 - 4 this would indicate directed non-disjunction of supernumeraries in the male and haploid transmission through the female. One plant with 29 chromosomes in all cells indicated complete elimination of supernumeraries in one parent and haploid transmission in the other. In an additional plant nine cells contained 31 chromosomes and one cell contained 30. This count of 30 indicates that the supernumerary univalent was lost prior to meiosis. In the last plant of this cross four pollen mother cells with 31 and five with 33 chromosomes were

Table 5: Transmission of supernumerary chromosomes in crosses of tetraploid crested wheatgrass.

No. of Cross	Description of Cross: Parents	Chromosome Number	No. of Progeny Plants	No. of Cells Observed	Mean No. of Supernumeraries in Progeny	No. of Cells with Chromosome No. of: 28	29	30	31	32	33	34
1	A x B	30 x 28	10	89	.48	46	43					
2	A x C	30 x 28	9	79	1.00		79					
3	B x A	28 x 30	10	91	1.09	38	6	47				
4	C x A	28 x 30	10	96	1.99	11		64	21			
5	A x D	30 x 30	10	94	2.92		8	1	80		5	
6	E x C	33 x 28	10	105	2.30		12	65	20		8	
7	C x E	28 x 33	9	114	4.87		2	3	10	16	44	39
	Total		68	668		95	150	180	131	16	57	39

noted. Such mosaics may be the result of non-disjunction of supernumeraries in some mitoses during the plant development or in archesporial cells.

Crosses 6 and 7 are reciprocals of two plants with 28 and 33 chromosomes. Six progeny plants of cross 6 had 30 chromosomes, two had 31 and one each had 29 and 33. Assuming normal movement of supernumeraries to the poles at meiosis, equal numbers of 30 and 31 chromosome individuals would be expected. This was not observed and it appeared most probable that occasionally the univalent supernumerary chromosome was lost during macrosporogenesis. The plant with 33 chromosomes represented an instance of directed non-disjunction of supernumeraries towards the egg. In the plant with 29 chromosomes all but one of the additional chromosomes were eliminated.

In cross 7 two plants had a uniform chromosome number of 33 and two had a uniform number of 34. In the remaining five plants the chromosome numbers varied within plants and ranged from 29 to 31, 31 to 33, 32 to 33, 32 to 34, and 33 to 34 for the five plants. The plant with 29 to 31 chromosomes presumably represented the only mating to which the pollen contributed only three supernumeraries. In this plant 14 cells were counted, two with 29 chromosomes, three with 30, and nine with 31. Directed non-disjunction of the supernumeraries towards the male gamete was demonstrated by the eight remaining plants. Variations in counts within plants indicated unequal distribution and some elimination of supernumeraries.

Agronomic Significance of Supernumerary Chromosomes in Crested Wheatgrass

Fertility, forage yield, and height in diploid controlled cross progenies

Table 6 includes a summary of agronomic data for diploid crosses listed in Table 4. Crosses are listed in order of parental chromosome combinations.

Table 6: Mean fertility, weight, and height in progenies of controlled crosses in diploid crested wheatgrass.

Cross	Mean No. of Supernumerary Chromosomes	Fertility (Percent)	Green Weight (lbs./plant)	Height (inches)
16 x 14	1.00	53.7	.68	25.3
18 x 14	2.11	47.1	.56	28.8
16 x 16	2.74	32.6	.48	23.1
14 x 18	3.40	48.7	.55	30.4
18 x 18	4.99	24.1	.37	26.5

Fertility and weight generally decreased and height increased as the mean number of supernumeraries in the population increased. This test did not include check varieties. The Fairway variety which is void of supernumeraries, generally averages 65 percent fertility. Critical evaluations were obtained from comparisons between progenies of reciprocal crosses which formed part of the data in Table 6. Data for individual crosses are presented in Table 7.

Table 7: Effect of supernumerary chromosomes in progenies of reciprocal crosses in diploid crested wheatgrass.

Cross	Mean No. of Supernumerary Chromosomes	Fertility (percent)	Green Weight (lbs./plant)	Height (inches)
D x I	1.77	61.5	.54	28.3
I x D	3.27	61.6	.52	27.6
E x I	1.98	54.5	.63	30.8
I x E	3.72	52.6	.68	30.0
E x J	2.00	45.8	.57	29.6
J x E	3.44	46.0	.51	31.4
D x J	2.00	36.0	.48	29.5
J x D	4.00	41.5	.63	32.6
G x J	2.00	48.6	-	-
J x G	3.37	48.9	-	-
G x I	2.00	58.7	-	-
I x G	2.59	41.9	-	-

Seven to ten individual plants were evaluated for each cross. The differences between reciprocals were tested for significance by means of t-tests. Differences in fertility were non-significant. Since differences in fertility between progenies with one common parent (D x I vs. E x I, D x I vs. D x J etc.) were significant in some cases, it appeared that in these populations variation in fertility was of genetic nature and was not influenced by supernumerary chromosomes.

Differences in plant weight were not significant for reciprocal crosses nor for crosses with one common parent. Coefficients of variability for plant weight were much larger than for fertility. Therefore larger populations would be

required to demonstrate significant differences. The progenies J x E and J x D were significantly taller than the reciprocals and this increase in height may be attributed to supernumerary chromosomes.

Fertility and height in tetraploid controlled cross progenies

The progenies used for the study of the transmission of supernumerary chromosomes, Table 5, were evaluated for fertility and height. Plant weights were not recorded because cuttings had been taken from these plants in the previous fall and this treatment introduced additional variation in plant size. The data are included in Table 8.

Table 8: Fertility and height in progenies of controlled crosses in tetraploid crested wheatgrass.

Cross	Mean Number of Supernumerary Chromosomes	Fertility (percent)	Height (inches)
A x B	.48	45.2	37.3
B x A	1.09	59.2	36.6
A x C	1.00	50.0	36.1
C x A	1.99	61.3	36.2
E x C	2.30	52.9	39.8
C x E	4.87	48.6	39.9
A x D	2.92	49.4	40.1

Differences in fertility between reciprocal crosses were significant in all three crosses. Progenies of the B x A and C x A crosses had better fertility than the reciprocals and

they also had a higher number of supernumeraries. These progenies contained supernumeraries in even numbers while the reciprocals contained them in odd numbers. In the progenies of the reciprocal cross A x B eight plants had no supernumeraries, seven plants had one, and five plants had two. The mean fertility in these three groups was 54.7 percent, 46.5 percent and 56.1 percent respectively. Fertility was significantly lower in the 29 chromosome group. It appeared therefore that fertility was depressed in this cross by one supernumerary chromosome but not by two.

In the other progenies similar groupings were not made. The chromosome numbers were similar in all plants of a cross, in which case the comparison of the reciprocals was adequate. Plant height was not influenced by the number of supernumeraries in these populations.

Fertility, forage yield, seed yield, and height of selected parents and their open-pollination progenies in tetraploid crested wheatgrass.

a. Fertility

Test 1 included 17 progenies of S-841 and 12 of S-1333 which were used for detailed analyses of fertility. Test 2 included 26 progenies of S-841 and six of the S-1333. The S-841 progenies of each test were analysed independently, whereas the S-1333 progenies of both tests were analysed

together. The parent data from test 4 were considered in the same manner. Because a few of the parental clones failed to establish in test 4, the number of parents involved in the variance analyses does not in all cases correspond with number of progenies used.

The parents of test 1, belonging to S-841 were included in four chromosome groups. Groups 1 and 2 each included three parents. Plants of group 1 had 28 meiotic chromosomes, plants in group 2 had 29. Group 3 included seven parents with 30 meiotic chromosomes. Group 4 included four parents, all having 31 chromosomes.

The analysis of variance and the components of variance of fertility of parent plants are included in Table 9.

Table 9: Analysis of variance and variance components of fertility in S-841 parents of test 1.

Source	Degrees of Freedom	Mean Square	Components of Variance ‡	Variance in % of total
Total	169	90.02	80.96	100.0
Chromosome groups	3	1922.98*	19.12	23.6
Parents within groups	13	336.83**	27.82	34.4
Clones within parents	68	42.67*	8.56	10.6
Spikes within clones	85	25.45	25.45	31.4

* and ** indicate significance at the five and one percent levels respectively. ‡ Components of variance were determined as indicated in Table 1 using the following coefficients:

k = 2	k3 = 168/169	r2 = 160/169
k1 = 2	r = 10	s = 61.18
k2 = 2	r1 = 10	s1 = 122.36/169

Significant differences in fertility occurred between clones within parents, between parents within chromosome groups and between chromosome groups. The cause of the large variance due to spikes is not clear. Variance between clones within parents was relatively unimportant while parents within chromosome groups represented the largest single variance component.

Table 10 includes the analysis of variance for fertility in the open-pollination progenies of these parents.

Table 10: Analysis of variance and variance components of fertility in open-pollination progenies of S-841 in test 1.

Source	Degrees of Freedom	Mean Square	Components of Variance	Variance in % of total
Total	509	309.16	309.15	100.0
Chromosome groups	3	2376.56	7.48	2.4
Progenies within groups	13	1107.57**	19.09	6.2
Plants within progenies	238	500.04**	216.60	70.1
Spikes within plants	255	65.98	65.98	21.3

k = 2	k3 = 508/509	r2 = 480/509
k1 = 2	r = 30	s = 121.17
k2 = 2	r1 = 30	s1 = 363.6/509

In the open-pollination progenies significant differences in fertility occurred between individual plants within progenies and between progenies within groups. The differences between chromosome groups were not significant. Variance due to plants within progenies represented the main variance component.

Fertility data for S-841 parents and progenies of test 2, for S-1333 parents and progenies of tests 1 and 2, and for Summit selections and progenies in tests 5 and 3 were analysed in the same manner. Analysis of variance tables are included in Appendices A, B, and C. These analyses showed highly significant differences in fertility between clones within parents and between parents within groups, but not between chromosome groups. Similarly, differences between plants within progenies and between progenies within groups were highly significant. The main variance components were parents within groups and plants within progenies. Variance due to spikes within plants again was smaller in the test of progenies than in the test of parents.

Table 11 includes the mean variance components in percent for parents of tests 4 and 5 and for progenies of test 1, 2, and 3.

Table 11: Pooled variance components in percent for all parents and open-pollination progenies.

Parents		Progenies	
Source	Variance	Source	Variance
Chromosome groups	8.1	Chromosome groups	.5
Parents within groups	46.5	Progenies within groups	9.5
Clones within parents	18.3	Plants within progenies	75.6
Spikes within clones	27.1	Spikes within plants	14.4
Total	100.0	Total	100.0

Spikes contributed 27.1 percent of the total variance of parents as compared to 14.4 percent of the total variance of progenies. Better pollination conditions in the progeny tests may, in part, account for the smaller variance component for spikes. However, since total variance in the progeny tests was larger than in the test of parents percentage values are not comparable. The comparison of the variance component for parents within groups with that for chromosome groups showed the importance of the genetic constitution of the parents in determining fertility. Variation due to chromosome groups was present but was relatively unimportant.

Plants within progenies were the main source of variation in tests of open-pollination progenies. This was largely genetic variance, but in part it may be due to supernumerary chromosomes and to within plot environmental effects. Variance due to chromosome groups was negligible. This was expected because it

may be assumed that some plants within all progenies contained supernumeraries. Consequently part of the fertility variance due to supernumeraries would be included in the variance components for plants within progenies and in the component for progenies within chromosome groups.

In Table 12 the mean fertilities of the parents of test 1 and 2 are given by chromosome groups.

Table 12: Mean fertility of S-841 and S-1333 parents according to chromosome groups. Fertility expressed as percentages.

Groups and Chrom. No.	S-841 test 1	S-841 test 2	S-1333 test 1 and test 2	Group Means	Coefficients of Variability
1 - 20	74.54 (3)*	64.31 (3)	66.69 (8)	67.86 (14)	11.25%
2 - 29	60.42 (3)	62.67 (8)	46.53 (3)	58.72 (14)	28.19%
3 - 30	68.16 (7)	64.80 (5)	55.06 (3)	64.42 (15)	16.62%
4 - 31 *	47.60 (4)	61.98 (2)	--	52.39 (6)	27.61%

* Bracketed values refer to the number of parents involved in the respective means.

Differences in fertility between chromosome groups were significant only for S-841 parents of test 1. However group means indicate a considerable loss in fertility due to supernumeraries, particularly in the groups with uneven numbers of additional chromosomes. In addition the coefficients of variability for these groups were much larger than those for the group without supernumeraries and for the group with a supernumerary pair. Coefficients of variability represent the standard deviations in percent of the means.

Mean fertilities of open-pollination progenies of parents included in the foregoing table are included in Table 13.

Table 13: Mean fertility of S-841 and S-1333 open-pollination progenies according to chromosome groups of their female parents.

Groups and Chrom. No.	S-841 test 1	S-841 test 2	S-1333 test 1 and test 2	Group Means	Coefficients of Variability
1 - 28	55.37 (3)*	57.92 (3)	51.58 (8)	53.75 (14)	19.12%
2 - 29	38.81 (3)	57.86 (8)	44.55 (3)	50.92 (14)	20.50%
3 - 30	53.02 (7)	49.27 (5)	53.49 (3)	51.86 (15)	16.66%
4 - 31 +	52.58 (4)	54.26 (2)	--	53.14 (6)	15.86%
Summit check	test 1: 44.99	test 2: 42.43	Nordan check	test 1: 41.14	test 2: 44.44

* Bracketed values refer to the numbers of progenies involved in each mean.

Variance analyses indicated that differences in fertility between these groups were non-significant. This is shown by comparisons of the group means in Table 13. However coefficients of variability for progeny groups were fairly similar, which was not the case in parental groups.

Table 14 includes mean fertility of the selected Summit plants in test 5, mean fertility of their open-pollination progenies in test 3, and coefficients of variability, according to parental chromosome groups.

Table 14: Mean fertility of selected Summit plants and open-pollination progenies according to chromosome groups.

Groups and Chrom. No.	Parents		Progenies	
	Fertility	C.V.	Fertility	C.V.
1 - 28	53.62 (10)	25.2%	41.40 (10)	19.0%
2 - 29	56.55 (13)	20.8%	40.28 (13)	30.9%
3 - 30	55.42 (6)	17.8%	38.63 (6)	23.5%
4 - 31	49.48 (4)	20.8%	33.54 (4)	28.1%
			Summit check 29.54 Nordan check 32.80	

In this material the differences in fertility between groups were less than in the S-841 and S-1333 material (Tables 12 and 13). Similarly the coefficients of variability for the parent data did not show the greater variability of plants with odd numbers of supernumeraries as was observed in Table 12. However, progenies of plants with odd numbers of supernumeraries were more variable.

b. Seed yield.

Seed yields were taken on the three tests of open-pollination progenies. In test 1 the plot yields required adjustment for block effects but according to the co-variance analysis no correction for missing plants was needed. Test 2 showed a significant regression of yield on numbers of plants

per plot and yields were corrected by co-variance methods. The test 3 data did not require stand corrections.

The results of test 1 and 2 are included in Table 15. The breakdown into strains and chromosome groups is similar to that used for the fertility data. However seed yields for strain S-1333 are presented separately for test 1 and test 2.

Table 15: Mean seed yields of open-pollination progenies of S-841 and S-1333 according to parental chromosome groups. Yields are presented in pounds per acre.

Groups and Chrom No.	S-841		S-1333		Group Means	Coefficients of Variability
	test 1	test 2	test 1	test 2		
1 - 28	336 (3)	430 (3)	320 (5)	354 (3)	354 (14)	12.4%
2 - 29	228 (3)	344 (8)	294 (3)	--	308 (14)	26.5%
3 - 30	296 (7)	346 (5)	--	320 (3)	317 (15)	11.2%
4 - 31 +	298 (4)	333 (2)	--	--	309 (6)	32.1%
Nordan check:	test 1	242	Summit check:	test 1	329	
	test 2	250		test 2	243	

Highest seed yields were produced by progenies of plants free of supernumerary chromosomes. These progenies yielded significantly more than those included in the 30 chromosome group, but not more than those in the 29 and 31 chromosome groups. Groups 1 and 3 showed less variability than groups 2 and 4.

Table 16 presents the mean seed yields obtained from the open-pollination progenies entering test 3, grouped according to the chromosome numbers of the female parents.

Table 16: Mean seed yields of open-pollination progenies of selected Summit parents according to parental chromosome groups. Yields are given in pounds per acre.

Groups and Chrom No.	Mean Yield	Number of Progenies	Coefficients of Variability
1 - 28	427	10	15.76%
2 - 29	415	13	31.50%
3 - 30	398	6	24.97%
4 - 31	352	4	18.57%
Summit check	434		
Nordan check	192		

The analyses of variance for the entire test showed significant differences between seed yields of individual progenies. However t-tests failed to show significant differences between any pair of progeny groups although there was a trend towards lower seed yield with an increase in the chromosome number of the female parent. The coefficients of variability showed that group 1 was the most uniform and group 2 the most variable.

c. Forage yield.

Forage yields, expressed in tons of dry matter per acre were recorded in 1959 for tests 1 and 2 and in 1960 for tests 2 and 3. In 1959 moisture conditions were below normal and yields were low, whereas in 1960 excellent growth was obtained. In test 1, 3.7 percent of plants were missing compared with

7.95 percent in test 2. The co-variance analyses showed significant regressions of yield on number of plants for tests 1 and 2 in 1959 and for test 2 in 1960. The regression coefficient calculated for test 1 was +.0686 and it was significant at the five percent level. For test 2 the regression was significant at the one percent level in 1959 and 1960, the coefficients being -.0331 and + .1195 respectively. Thus in the year with limited moisture supply the plots of test 2 with missing plants showed a yield advantage, whereas, in the year with favorable moisture these same plots were at a disadvantage. Yields were corrected by co-variance analysis for each year. Forage data of test 3 were not corrected for missing plants, since only 1.59 percent of the plants were missing. The lattice analysis was carried out with correction for block effects.

Tests 1 and 2 did not show significant differences between forage yields of progenies in either year. However, in test 3 significance was shown at the one percent level. The progenies were again grouped according to the chromosome numbers of the female parents. Fertility and seed yields were reported for progenies of parents for which fertility data had been obtained (Tables 13 and 15). Forage yields are presented for the progenies of all parents whose chromosome numbers had been determined. Therefore the numbers of progenies in the various groups are in some cases larger than those in Tables 13 and 15 which report fertility and seed yields. Yields of tests 1 and 2 for 1959 are included in Table 17 and yields of test 2 for 1960 are included in Table 18.

Table 17: Mean forage yields of open-pollination progenies of S-841 and S-1333 according to parental chromosome groups, 1959. Yields are given in tons dry matter per acre.

Groups and Chrom. No.	S-841		S-1333		Group Means	Coefficients of Variability
	Test 1	Test 2	Test 1	Test 2		
1 - 28	.93 (3)	1.01 (6)	1.04 (8)	.95 (3)	1.00 (20)	16.15%
2 - 29	.86 (3)	.92 (13)	.95 (3)	--	.92 (19)	9.89%
3 - 30	.95 (7)	.96 (6)	.94 (2)	.97 (3)	.96 (18)	11.25%
4 - 31 +	.93 (4)	.97 (3)	--	--	.95 (7)	11.89%
Nordan check:	test 1 .98		Summit check:		test 1 1.00	
	test 2 .68				test 2 .69	

Table 18: Mean forage yields of open-pollination progenies of S-841 and S-1333 according to parental chromosome groups, 1960. Yields are given in tons dry matter per acre.

Groups and Chrom. No.	S-841	S-1333	Group Means	Coefficients of Variability
1 - 28	2.08 (6)	2.01 (3)	2.06 (9)	5.97%
2 - 29	2.03 (13)	--	2.03 (13)	6.10%
3 - 30	2.06 (6)	2.20 (3)	2.12 (9)	5.70%
4 - 31 +	2.02 (3)	--	2.02 (3)	9.75%
Nordan check:	1.67		Summit check:	1.75

Differences in yields of progeny groups were not significant in 1959 or 1960 according to t-tests. In test 1 the yields of check varieties were approximately equal to the mean yield of the progenies. The mean progeny yields of test 2 exceeded those of the checks in both years. The coefficients of variability within groups were smaller for forage yield than for seed yield. In addition the much larger variability in seed yields of groups 2 and 4 is not paralleled by a similarly greater variability of forage yields.

The forage yields for test 3 are included in Table 19.

Table 19: Mean forage yields of open-pollination progenies of selected Summit plants according to chromosome groups. Yields are given in tons dry matter per acre.

Groups and Chrom. No.	Mean Yield	Number of Progenies	Coefficients of Variability
1 - 28	1.73	10	9.88%
2 - 29	1.62	13	10.12%
3 - 30	1.71	6	14.67%
4 - 31	1.60	4	16.77%
Nordan check	1.15	Summit check	1.76

In this test the differences between groups of progenies were again not statistically significant and the coefficients of variability were smaller than the corresponding coefficients for seed yield (Table 16). The analysis of variance, however, showed

significance at the one percent level for yields of individual progenies. Nine individual progenies excelled Summit in forage yield.

While trends towards lower fertility and lower seed yields were noted in progenies of parents with supernumerary chromosomes, a similar trend was not shown with respect to forage yield. Similarly, the greater variability in fertility and seed production, found among progenies of plants with odd numbers of supernumeraries, was not paralleled by correspondingly greater variability in forage production.

d. Plant height

Plant height was recorded in tests 1 and 2 for 1959 and in test 3 for 1960. All plants within each plot were measured and plot means calculated. These plot values were used in the analyses of variance. Tests 1 and 2 required adjustment for block effects but in test 3 block effects were not significant. Because the mean height in test 2 was somewhat larger than in test 1, height data are presented in Table 20 for individual tests.

Table 20: Mean plant height in inches of open-pollination progenies of S-841 and S-1333 according to parental chromosome groups.

Groups and Chrom. No.	Height		Group Means	Coefficients of Variability
	S-841	S-1333		
Test 1: 1 - 28	28.29 (3)	29.25 (7)	28.97 (10)	5.35%
2 - 29	29.00 (3)	30.07 (3)	29.54 (6)	3.00%
3 - 30	29.70 (7)	29.43 (2)	29.64 (9)	4.38%
4 - 31 +	29.32 (4)	--	29.32 (4)	5.01%
Test 2: 1 - 28	31.80 (5)	31.88 (3)	31.83 (8)	3.51%
2 - 29	32.03 (13)	--	32.03 (13)	3.49%
3 - 30	31.28 (5)	32.42 (3)	31.70 (8)	3.28%
4 - 31 +	32.70 (3)	--	32.70 (3)	4.19%
Summit check: test 1 25.86 test 2 26.21			Nordan check: test 1 27.83 test 2 27.39	

In the S-841 and S-1333 progenies no significant effects of supernumerary chromosomes on plant height could be detected by means of t-tests. Progenies of plants with additional chromosomes were slightly taller than those of plants without supernumeraries. Progenies within all groups showed low variability.

Similar results were obtained in test 3 as shown in Table 21. In this test the difference in height between groups 2 and 4 was significant at the five percent level of probability. However the latter group included only four progenies.

Table 21: Mean plant height in inches of open-pollination progenies of selected Summit plants, according to parental chromosome groups.

Groups and Chrom No.	Mean Height	Coefficients of Variability
1 - 28	37.66 (10)	3.45%
2 - 29	36.52 (13)	5.14%
3 - 30	37.21 (6)	4.17%
4 - 31	38.10 (4)	1.60%
Summit check	35.88	
Nordan check	35.56	

e. Parent-progeny relationships

Regressions of progeny on parent for fertility were determined for the data of tests 1 and 2 combined and for test 3. In addition, the relation of seed yield to fertility was ascertained. Regression coefficients were calculated for entire populations as well as for individual chromosome groups. In Table 22 the respective coefficients are presented for progenies included in tests 1 and 2 and their parents. Regressions calculated on percentage data are compared to those obtained on the transformed values. Standard errors of regressions and t-values also are included.

Table 22: Regressions of progeny on parents for fertility, S-841 and S-1333 strains.

Groups and Chrom. No.	No. of Comparisons	Percentage data			Transformed data		
		byx	Se	t	byx	Se	t
1 - 28	19	.4749	.2663	1.783	.4301	.2517	1.708
2 - 29	17	.3013	.1348	2.235*	.2911	.1265	2.301*
3 - 30	16	.0839	.2046	.410	.0872	.1979	.440
4 - 31 +	7	.1667	.3002	1.800	.1658	.2971	.558
Average	59	.2524	.0882	2.862**	.2463	.0843	2.921**

Regression coefficients based on transformed values agreed very closely with those calculated from percentage data. It appeared that transformation was not necessary in the analysis of these data. Standard errors for regressions based on transformed data were somewhat smaller than those for percentage data.

Table 23 includes similar data for the Summit progenies included in test 3 and their parents in test 5.

Table 23: Regressions of progenies on parents for fertility, Summit selections.

Groups and Chrom No.	No. of Comparisons	Percentage data			Transformed data		
		byx	Se	t	byx	Se	t
1 - 28	10	.3319	.1756	1.890	.3327	.1757	1.893
2 - 29	13	.7168	.2355	3.043*	.6698	.2474	2.707*
3 - 30	6	.8124	.2179	3.728*	.7940	.2096	3.788*
4 - 31	4	.2984	.6161	.484	.3156	.6637	.475
Average	33	.5288	.1260	4.196**	.5304	.1270	4.176**

As in the previous table regression coefficients based on percentage data were very similar to those based on transformed values. The average regressions showed highly significant relationships for fertility of parents and their open-pollination progenies in S-841 and S-1333, and in Summit selections. For the populations of test 1 and 2 an average regression value of .2463 when doubled indicated a heritability value of 49.26 percent. In the Summit selections a higher heritability estimate was indicated by a regression coefficient of .5304 $\pm$ .1270.

Individual group regressions were significant for group 2 in Table 22 and for groups 2 and 3 in Table 23. Tests of significance for differences between group regressions were conducted in the manner described by Snedecor (97). The analysis tables are included in Appendix D. For these calculations the transformed data were used. The analyses show

that for both sets of data differences between group regressions were not significant. Inheritance of fertility therefore did not appear to be influenced by supernumerary chromosomes in the female parents.

The relationship between seed yield in pounds per acre and fertility expressed in percentages was determined by means of regression analyses. On the basis of these regressions the reliability of fertility indices in selection of parents with good combining ability for seed production could be evaluated. Table 24 includes regression coefficients, standard errors of regressions, and t-values for the combined data of S-841 and S-1333 populations.

Table 24: Regression of progeny seed yield on fertility of parents and fertility of progenies in S-841 and S-1333.

Groups and Chrom. No.	No. of Comparisons	Regression on Parent Fertility byx	Se	t	Regression on Progeny Fertility byx	Se	t
1 - 28	19	3.0905	1.6025	1.928	4.7290	.9322	5.072**
2 - 29	17	1.5916	1.1729	1.356	6.1416	1.3159	4.667**
3 - 30	16	.8180	.8161	1.002	- .8258	1.0733	.768
4 - 31 +	7	4.2583	2.8716	1.482	9.3168	2.7272	3.416*
Average	59	2.2282	.6163	3.615**	4.4827	.7528	5.954**

The average regressions of progeny seed yield on parent and progeny fertility were highly significant. Regressions also

indicate that one percent gain in fertility in the parents corresponded to a gain in progeny seed yield of 2.23 pounds per acre. As expected, a higher relationship was observed between progeny seed yield and progeny fertility than between progeny seed yield and parent fertility.

Similar regressions for the selected Summit population are included in Table 25.

Table 25: Regressions of progeny seed yield on fertility of parents and fertility of progenies for Summit selections.

Groups and Chrom. No.	No. of Comparisons	Regression on Parent Fertility byx	Se	t	Regression on Progeny Fertility byx	Se	t
1 - 28	10	1.4974	1.6780	.892	6.4597	1.8618	3.469**
2 - 29	13	4.6273	3.0453	1.519	8.7449	1.7380	5.031
3 - 30	6	5.8061	4.1230	1.408	8.5447	3.4130	2.503
4 - 31	4	5.4625	2.2991	2.375	3.9576	4.0300	.982
Average	33	3.7925	1.3628	2.783**	7.9948	.9657	8.278**

In this population the average regressions were highly significant and the coefficients were larger than in Table 24. This is due to the fact that fertility in the Summit population was somewhat lower than in S-841 and S-1333, while seed yields in test 3 were higher than in tests 1 and 2. These results indicate that fertility indices are a reliable basis of selection for

plants with high seed production potential. Tests of significance for differences between the group regressions in Tables 24 and 25 were conducted as illustrated previously. In all instances these differences were not significant.

By means of correlation analyses the relationships between some of the other characteristics investigated in this study were determined. The correlation coefficients are included in Table 26. These correlations were calculated on the complete data of tests 1 and 2 and included 64 comparisons, and of test 3 which included 36 comparisons. The correlation between 1958 and 1959 fertility of test 1 involved 52 pairs of observations.

Table 26: Correlation coefficients for forage yield, seed yield, height, fertility, and year of testing.

Comparison	Correlation Coefficient
Forage yield and seed yield:	
Test 1 1959	+ .5452**
Test 2 1959	+ .7135**
Test 3 1960	+ .5726**
Forage yield and height:	
Test 1 1959	+ .1108
Test 2 1959	+ .6246**
Test 3 1960	+ .5338**
Forage yield 1959 and Forage yield 1960: Test 2	+ .7178**
Fertility 1958 and Fertility 1959: Test 1	+ .6925**

Significant positive associations were observed between forage yield and seed yield. Correlations between forage yield and height were positive in all tests but significant only for test 2 and 3. The year to year correlations for forage yield and fertility were highly significant.

DISCUSSION

Two of the diploid and all of the tetraploid populations of this study contained plants with supernumerary chromosomes. In the diploid strain S-3541 plants with supernumeraries were observed at a frequency of 95.8 percent, while in tetraploids their frequency ranged from 36.9 percent in S-1333 to 88.5 percent in Nordan. In most other grasses noted as having supernumeraries a lower frequency of 5 to 50 percent was observed (8, 12, 62, 79). Supernumeraries occurred with frequencies as high as those observed in crested wheatgrass only in a diploid strain of Poa alpina (57) and in certain wild populations of rye (64). As in corn, rye, and other grasses (4, 12, 62, 64) plants of crested wheatgrass with even numbers of supernumeraries were more common than plants with uneven numbers.

In crested wheatgrass, as in previously reported species, the frequency of supernumeraries did not depend on the degree of polypoidy. Müntzing (64, 65) stated that supernumeraries in rye and certain other grasses were of ancient origin. Various authors (8, 12, 25) agreed that ecological factors influenced the distribution of these additional chromosomes, but definite relationships could not be established. The different origin and area of distribution may therefore be responsible for the absence of supernumeraries in Fairway and for their presence in S-3541 and S-5239. Since the genotypes of individual plants influenced the degree of transmission, it is possible that genetic factors prevent the occurrence of supernumerary chromosomes in Fairway.

Plants of diploid crested wheatgrass contained supernumeraries in pollen mother cells, in primary roots, and in stem meristem. As in Sorghum purpureo-sericeum (18) and in Poa alpina (57) adventitious roots were without supernumeraries. Studies by Knowles (42) indicated that tetraploid crested wheatgrass plants with supernumeraries at meiosis contained the normal complement in adventitious roots.

Supernumerary chromosomes in crested wheatgrass differed from normal chromosomes in many respects. As in most other species, supernumeraries paired with themselves but not with chromosomes of the basic set. They were readily distinguished on the basis of size in diploid crested wheatgrass (Fig. 2-9). Generally they were one-third to one-half the size of normal chromosomes. Supernumeraries were distinguished on the same basis in most other grass species, but in rye and Festuca pratensis various size classes were reported (6, 12, 67, 68). The basic chromosomes of tetraploid crested wheatgrass appeared more variable in size and consequently supernumeraries were not as readily distinguished. The heterochromatic nature is the most universal characteristic of supernumeraries. However, with acetocarmine no differential staining reaction could be detected in supernumeraries of crested wheatgrass.

The behavior of supernumeraries during meiosis was similar to the behavior of basic chromosomes. Generally the reductional division at anaphase I was followed by the equational division at anaphase II. Precocious divisions of supernumerary univalents at anaphase I (Fig. 9) and lagging

univalents were not as common in crested wheatgrass as in many other species (12). Lagging univalents were usually included in the daughter nuclei and micronuclei seldom occurred.

Supernumerary chromosomes were transmitted in the same manner in crested wheatgrass as in numerous other grass species (7, 9, 12, 18, 36, 87). In pollen, directed non-disjunction of supernumeraries towards the gametophyte occurred with a frequency of approximately 70 percent. Transmission through the egg generally took place in haploid numbers. Deviations from this mode of transmission appeared to be influenced by the genotypes of the parents and by the number of supernumeraries involved.

This study showed that elimination was low in plants with small numbers of supernumeraries, but became more pronounced as the number of supernumeraries increased. The increase in numbers of supernumeraries, caused by directed non-disjunction towards the male gametophyte thus appeared to be paralleled by higher elimination. As a result, an equilibrium was reached in natural populations and plants with more than four supernumeraries were not frequent.

It is not possible with these limited data to form definite conclusions regarding the agronomic significance of supernumerary chromosomes in diploid crested wheatgrass. Fertility and forage yield generally decreased as the number of supernumeraries increased. Detrimental effects were

pronounced only in progenies with more than four supernumeraries. Plants were very specific in their ability to produce fertile progenies and it appeared that fertility depended mainly on genetic factors. Since no beneficial effects of supernumeraries could be detected, it seems desirable to eliminate plants with supernumeraries from breeding programs. Bosemark (12) observed various agronomic traits in Festuca pratensis. As in diploid crested wheatgrass deterimental effects of supernumeraries were not significant in most instances.

Progenies of controlled crosses in tetraploid crested wheatgrass revealed a significant reduction in fertility when uneven numbers of supernumeraries were present. One supernumerary bivalent did not cause a reduction in fertility. Meiosis in pollen mother cells was normal, even in plants with four or more supernumeraries. It is concluded therefore that significantly lower fertility was the result of irregularities in macrosporogenesis or of abnormal embryo development. Therefore it appears necessary that detailed studies of fertility be conducted in conjunction with cytological investigations of both male and female flower parts.

Studies of the effects of supernumerary chromosomes, on fertility of selected plants were inconclusive. In various selected populations plants with uneven numbers of supernumerary chromosomes had considerably lower fertility than plants without supernumeraries or plants with a supernumerary pair. Differences in fertility between chromosome groups however

were not significant in most instances, mainly because of extreme variability within the 29 and 31 chromosome groups. Variance analyses showed that differences between plants were the main source of fertility variance and that chromosome groups were relatively unimportant.

Fertility data of open-pollination progenies, grouped according to the chromosome numbers of the female parents, indicated that the contribution of chromosome groups to the total variance was negligible. In addition, differences in variability within groups were not pronounced. Plants within progenies were the main source of variance, indicating the importance of the genotypes in determining fertility. In agreement with these observations heritability estimates based on doubled progeny-parent regressions (49) were also fairly high. These regressions were considerably higher in Summit than in S-841 and S-1333. This suggests that inbreeding has occurred in the Summit variety. Heritability was not significantly different in various chromosome groups and this may indicate that supernumeraries are genetically inert.

Marked reductions in seed yield were noted in open-pollination progenies of plants with supernumeraries as compared to progenies of plants without supernumeraries. In the S-841 and S-1333 progenies, yields in the 30 chromosome group were significantly lower than in the 28 chromosome group. Extreme variability in seed yields of progenies was shown for the 29

and 31 chromosome groups. Seed yields of open-pollination progenies thus indicated considerably lower combining ability of plants with supernumeraries. On the basis of regressions of seed yield on fertility it is concluded that fertility indices are very valuable for the initial selection of plants with high seed production potential.

Forage yield and plant height of open-pollination progenies were less affected by supernumerary chromosomes than was fertility. In most tests, however, progenies of plants without supernumeraries ranked highest in forage yield. The slight increase in height of progenies of plants with supernumeraries may not reflect direct effects of these chromosomes. It was noted that plants with low seed set maintain vegetative growth somewhat longer than plants with high seed set. Increased height may therefore be the result of lower seed production.

These studies revealed marked detrimental effects of supernumerary chromosomes on fertility of selected plants and of controlled cross progenies with uneven numbers of additional chromosomes. Similarly seed yields in open-pollination progenies of plants with supernumeraries were considerably lower than those of plants with the normal complement. It would appear desirable to select against supernumeraries even though in most instances the detrimental effects were not statistically significant. Since high fertility was one of the main objectives in the selection of parents, it appears likely that the various

populations of selections included only highly fertile segregates. Consequently the loss in fertility due to supernumeraries, although not statistically significant, must be considered extensive.

The reduction in seed yield of open-pollination progenies of plants with supernumeraries was marked in all tests but significant only in one instance. It is concluded, however, that effects of supernumeraries are in fact more pronounced than shown by tests of open-pollination progenies, as conducted here. Open-pollination progenies of plants with, and of plants without supernumeraries presumably contained numerous individuals with additional chromosomes because a large proportion of the paternal parents contained supernumeraries. Therefore progenies in the 28 chromosome group do not represent a true check. Seed yields of this group presumably are reduced to some extent by supernumerary chromosomes, and the use of this group as a basis of comparisons would tend to minimize their effects.

Better evaluations of the agronomic significance of supernumeraries in crested wheatgrass could have been obtained by more extensive use of controlled cross progenies. Plants representing the various chromosome groups should be used as parents. On the basis of results of the transmission study the chromosome numbers of the progenies could be predicted with sufficient accuracy, and cytological examination of extensive populations would not be required. Results on agronomic

characteristics would be more precise than those from open-pollination progenies.

Two alternative methods of evaluating effects of supernumerary chromosomes may be suggested. Open-pollination progenies could be used, provided that individual progeny plants were studied cytologically and grouped according to chromosome number. This method would be very accurate but could only be applied to relatively small populations, because of the labor involved. Synthetics including only 28 chromosome plants also could be compared in successive generations with other synthetics of plants with supernumeraries. This approach is being taken and first generation seed of 13 synthetics will be produced in 1961. Several of these synthetics consist of plants originating from the same crosses but which differ in their chromosome numbers. Consequently genetic differences between these synthetics should be small and effects of supernumeraries should be detectable. Cytological examinations of the synthetics with supernumeraries in successive generations would also provide a measure of the increase in the number of supernumeraries from generation to generation.

Results of the present study strongly suggest that plants with supernumerary chromosomes should be eliminated from breeding programs. It is anticipated that additional studies in progress will provide more complete answers concerning the agronomic significance of supernumerary chromosomes in crested wheatgrass.

SUMMARY

1. Supernumerary chromosomes were observed at meiosis in diploid and tetraploid populations of crested wheatgrass. They were absent in the diploid variety Fairway but they were present with frequencies exceeding 95 percent in two diploid introductions. In the tetraploid populations their frequency ranged from 36.9 percent to 88.5 percent.
2. Plants of diploid S-3541 contained supernumeraries in pollen mother cells, in primary roots, and in stem tissues, but not in adventitious roots.
3. Supernumeraries were smaller than basic chromosomes and they did not appear to be heterochromatic. They paired with themselves but not with normal chromosomes. In diploid and tetraploid crested wheatgrass transmission of supernumeraries through the egg occurred in haploid numbers. In the pollen directed non-disjunction towards the gamete took place with a frequency of approximately 70 percent. The degree of transmission depended on the numbers of supernumeraries involved and on the genotypes of the parents. Elimination of supernumeraries was generally low but became more pronounced with an increase in their numbers.
4. Fertility, plant weight, and plant height were not significantly affected by supernumerary chromosomes in diploid progenies of controlled crosses. A trend towards reduced fertility and yield and increased height was apparent.

5. Tetraploid progenies of controlled crosses showed significantly lower fertility in plants with uneven numbers of supernumeraries. Plant height was not affected by supernumeraries.
6. Fertility of tetraploid selections with supernumeraries was considerably lower than that of plants without supernumeraries. The main source of fertility variance, however, was genetic. Seed yields in open-pollination progenies of plants with the normal chromosome complement were higher than those in progenies of plants with supernumeraries. In most instances these differences in fertility and seed yield were not statistically significant. Forage yield and height in open-pollination progenies did not indicate differential combining ability of parents in the various chromosome groups. Nevertheless it is concluded selection against supernumeraries should be conducted.
7. Alternative methods of evaluating the agronomic significance of supernumerary chromosomes in crested wheatgrass are suggested.

ACKNOWLEDGMENTS

The studies reported in this thesis were carried out in part at the Forage Crops Section, Research Station, Canada Department of Agriculture, Saskatoon, and in part at the Experimental Farm, Lacombe. Dr. J.L. Bolton, Officer in Charge at Saskatoon, and Mr. J.G. Stothart, Superintendent at Lacombe, provided facilities and equipment. Their assistance and that of other staff members is much appreciated.

The author wishes to express particular thanks to Dr. R.P. Knowles, Research Officer, Forage Crops Section, Research Station, Canada Department of Agriculture, Saskatoon. Dr. Knowles suggested the problem and offered guidance throughout the course of the study. His generous assistance in the preparation of this final report is much appreciated.

Dr. H.T. Fredeen, Head, Animal Husbandry, Experimental Farm, Lacombe, offered valuable advice on the statistical treatment of some of the data. The author wishes to thank Dr. Fredeen for his interest and advice.

REFERENCES

1. Berger, C.A., and E.R. Witkus. The cytology of Xanthisma texanum D.C. I. Differences in the chromosome number of root and shoot. Bull. Torrey Bot. Club 81:489-491, 1954.

2. Berger, C.A., R.M. McMahon, and E.R. Witkus. The cytology of Xanthisma texanum D.C. III. Differential somatic reduction. Bull. Torrey Bot. Club 83:377-382, 1955.

3. Berger, C.A., E.J. Feeley, and E.R. Witkus. The cytology of Xanthisma Texanum D.C. IV. Megasporogenesis and embryosac formation, pollen mitosis and embryo formation. Bull. Torrey Bot. Club 83:428-434, 1956.

4. Blackwood, M. The inheritance of B chromosomes in Zea mays. Heredity 10:353-366, 1956.

5. Böcher, T.W. Chromosome behavior and syncyte formation in Phleum phleoides (L.) Karst. Bot. Notiser, :353-368, 1950.

6. Bosemark, N.O. On accessory chromosomes in Festuca pratensis. I. Cytological investigations. Hereditas 40:346-376, 1954.

7. Bosemark, N.O. On accessory chromosomes in Festuca pratensis. II. Inheritance of the standard type of accessory chromosomes. Hereditas 40:425-437, 1954.

8. Bösemark, N.O. On accessory chromosomes in Festuca pratensis. III. Frequency and geographical distribution of plants with accessory chromosomes. Hereditas 42:189-210, 1956.

9. Bosemark, N.O. On accessory chromosomes in Festuca pratensis. IV. Cytology and inheritance of small and large accessory chromosomes. Hereditas 42:235-260, 1956.

10. Bosemark, N.O. Cytogenetics of accessory chromosomes in Phleum phleoides. Hereditas 42:443-466, 1956.

11. Bosemark, N.O. On accessory chromosomes in Festuca pratensis. V. Influence of accessory chromosomes on fertility and vegetative development. Hereditas 43:211-235, 1957.

12. Bosemark, N.O. Further studies on accessory chromosomes in grasses. Hereditas 43:236-297, 1957.

13. Catcheside, D.G. The genetics of B chromosomes in maize. Heredity 10:345-351, 1956.

14. Chennaveeraiah, M.S. and A. Löve. Occurrence of supernumerary chromosomes and chromosome fragments in Aegilops. Can. Jour. Gen. and Cytol. 1:26-33, 1959.

15. Comstock, R.E., and H.F. Robinson. The components of genetic variance in a population of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4:254-266, 1948.

16. Darlington, C.D., and L.F. LaCour. The detection of inert genes. Jour. Hered. 32:115-121, 1941.

17. Darlington, C.D., and L.F. LaCour. Hybridity selection in Campanula. Heredity 4:217-248, 1950.

18. Darlington, C.D., and P.T. Thomas. Morbid mitosis and the activity of inert chromosomes in Sorghum. Proc. Roy. Soc. London, B, 130:127-150, 1941.

19. Darlington, C.D., and M.B. Upcott. The activity of inert chromosomes in Zea Mays. Jour. Gen. 41:275-296, 1941.

20. Dewey, D.R. and K.H. Lu. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agron. Jour. 51:515-518, 1959.

21. Ehrendorfer, F. Akzessorische Chromosomen, Kreuzungsfertilitat und Polyploidie beim Achillea millefolium Komplex (Compositae). Die Naturwissenschaften 44:405-406, 1957.

22. Frȍst, S. The genetic effect of accessory chromosomes in Centaurea scabiosa. Hereditas 40:529-533, 1954.

23. Frȍst, S. The cytological behavior of accessory chromosomes in Centaurea scabiosa. Hereditas 42:415-431, 1956.

24. Frȍst, S. The inheritance of the accessory chromosomes in Centaurea scabiosa. Hereditas 43:403-422, 1957.

25. Frȍst, S. The geographical distribution of accessory chromosomes in Centaurea scabiosa. Hereditas 44:75-111, 1958.

26. Frȍst, S. Studies of the genetical effects of accessory chromosomes in Centaurea scabiosa. Hereditas 44:112-122, 1958.

27. Frȍst, S. The cytological behavior and mode of transmission of accessory chromosomes in Plantago serraria. Hereditas 45:191-210, 1959.

28. Frȍst, S., and G. Östergren. Crepis pannonica and Crepis conyzaefolia. Two more species having accessory chromosomes. Hereditas:45:211-214, 1959.

29. Grun, P. Variability of accessory chromosomes in native populations of Allium cernuum. Am. Jour. Bot. 46:218-224, 1959.

30. Hair, J.B. The origin of new chromosomes in Agropyron. Heredity 6 (sup.) :215-233, 1953.

31. Håkansson, A. Behavior of accessory rye chromosomes in the embryo-sac. Hereditas 34:35-39, 1948.

32. Håkansson, A. Embryology of Poa alpina plants with accessory chromosomes. Hereditas 34:233-247, 1948.

33. Håkansson, A. Supernumerary chromosomes in Godetia viminea. Hereditas 35:375-389, 1949.

34. Håkansson, A. Transmission of accessory chromosomes in Poa alpina. Hereditas 40:523-526, 1954.

35. Håkansson, A. Meiosis and pollen mitosis in rye plants with many accessory chromosomes. Hereditas 43:603-620, 1957.

36. Håkansson, A. Behavior of different small accessory rye chromosomes at pollen mitosis. Hereditas 45:623-631, 1959.

37. Hartung, M.E. Chromosome numbers in Poa, Agropyron, and Elymus. Am. Jour. Bot. 33:516-531, 1946.

38. Hill, H.D., and W.M.Meyers. Chromosome numbers in Bromus inermis Leyss. Jour. Am. Soc. Agron. 40:466-469, 1948.

39. Jacobs, P.A., and J.A. Strong. A case of human intersexuality having a possible XXY sex determining mechanism. Nature 183:302-303, 1959.

40. Janaki-Ammal, E.K. Chromosome diminution in a plant. Nature 1946:839-840, 1940.

41. Kempthorne, O. An introduction to genetic statistics. John Wiley and Sons Inc. New York. 1957.

42. Knowles, R.P. A study of variability in crested wheatgrass. Can.Jour. Bot. 33:534-546, 1955.

43. Lewis, H. The geographical distribution of supernumerary chromosomes in natural populations of Clarkia elegans Dougl. Genetics 35:674-675, 1950.

44. Lewis, H. The origin of supernumerary chromosomes in natural populations of Clarkia elegans. Evolution 5:142-157, 1951.

45. Lima-de-Faria, A. Disturbances in microspore cytology of Anthoxanthum. Hereditas 33:539-551, 1947.

46. Longley, A.E. Supernumerary chromosomes in Zea mays. Jour. Agric. Res. 35:769-784, 1927.

47. Longley, A.E. Chromosomes of maize from North American Indians. Jour. Agric. Res. 56:177-195, 1938.

48. Longley, A.E. The origin of diminutive B type chromosomes in maize. Am. Jour. Bot. 43:18-22, 1956.

49. Lush, J.L. Intra-sire correlations or regressions of offspring on dams as a mtehod of estimating heritability of characters. Proc. Am. Soc. An. Prod. 33:293-301, 1940.

50. Markarian, D., and J. Schulz-Schaeffer. A possible origin of supernumerary fragment chromosomes. Jour. Heredity 49:3-7, 1958.

51. Melander, Y. Accessory chromosomes in animals, especially in Polycelis tenuis. Hereditas 36:19-38, 1950.

52. Milinkovic, V. Accessory chromosomes in the roots of Poa alpina. Hereditas 43:583-588, 1957.

53. Müntzing, A. Genetical effects of duplicated fragment chromosomes in rye. Hereditas 29:91-112, 1943.

54. Müntzing, A. Cytological studies of extra fragment chromosomes in rye. I. Iso-fragments produced by misdivision. Hereditas 30:231-248, 1944.

55. Müntzing, A. Cytological studies of extra fragement chromosomes in rye. II. Transmission and multiplication of standard fragments and iso-fragments. Hereditas 31:457-477, 1945.

56. Müntzing, A. Cytological studies of extra fragment chromosomes in rye. III. The mechanism of non-disjunction at pollen mitosis. Hereditas 32:97-119, 1946.

57. Müntzing, A. Different chromosome numbers in root tips and pollen mother cells in a sexual strain of Poa alpina. Hereditas 32:127-129, 1946.

58. Müntzing, A. Accessory chromosomes in Poa alpina. Heredity 2:49-61, 1948.

59. Müntzing, A. Cytological studies of extra fragment chromosomes in rye. IV. The position of various fragment types in somatic plates. Hereditas 34:161-180, 1948.

60. Müntzing, A. Cytological studies of extra fragment chromosomes in rye. V. A new fragment type arisen by deletion. Hereditas 34:435-442, 1948.

61. Müntzing, A. Accessory chromosomes in Secale and Poa. Hereditas 35 (sup.):402-411, 1949.

62. Müntzing, A. Accessory chromosomes in rye populations from Turkey and Afghanistan. Hereditas 36:507-509, 1950.

63. Müntzing, A. Cyto-genetics of accessory chromosomes)B-chromosomes). Caryolgia 6 (sup.) :282-301, 1954.

64. Müntzing, A. Frequency of accessory chromosomes in rye strains from Iran and Korea. Hereditas 43:682-685, 1957.

65. Müntzing, A. Accessory chromosomes. Transactions Bose Research Institute 22:1-15, 1958.

66. Müntzing, A., and S. Akdik. The effect on cell size of accessory chromosomes in rye. Hereditas 34:248-250, 1948.

67. Müntzing, A., and A. Lima-de-Faria. Pachytene analysis of standard fragments and large iso-fragments in rye. Hereditas 35:253-268, 1949.

68. Müntzing, A., and A. Lima-de-Faria. Pachytene analysis of a deficient accessory chromosome in rye. Hereditas, 38:1-10, 1952.

69. Müntzing, A., and A. Lima-de-Faria. Pairing and transmission of a small accessory iso-chromosome in rye. Chromosoma 6:142-148, 1953.

70. Müntzing, A., and A. Nygren. A new diploid variety of Poa alpina with two accessory chromosomes at meiosis. Hereditas 41:405-422, 1955.

71. Müntzing, A., and R.Prakken. Chromosomal observations in rye populations. Hereditas 27:273-308.

72. Myers, W.M., and H.D. Hill. Studies of chromosomal associations and behavior and the occurrence of aneuploidy in autotetraploid grass species, orchard grass, tall oatgrass and crested wheatgrass. Bot. Gaz. 102:236-255, 1940.

73. Nielsen, E.L. Cytological disturbances influencing fertility in Bromus inermis. Bot. Gaz. 116:293-305, 1955.

74. Nygren, A. Poa timoleontis Heldr., a new diploid species of the section Bolbophorum A. and Gr. with accessory chromosomes only at meiosis. Kungl. Landbr. Hogsk. Ann. 23:489-495, 1957.

75. Östergren, G. Parasitic nature of extra fragment chromosomes. Bot. Notiser :157-163, 1945.

76. Östergren, G. Heterochromatic. B.-chromosomes in Anthoxanthum. Hereditas 33:261-296, 1947.

77. Paliwal, R.L., and B.B. Hyde. The association of a single B-chromosome with male sterility in Plantago coronopus. Am. Jour. Bot. 46:460-466, 1959.

78. Peto, F.H. Cytological studies in the genus Agropyron. Can. Jour. Res. 3:428-448, 1930.

79. Randolph, L.F. Genetic characteristics of the B-chromosomes in maize. Genetics 26:608-631, 1941.

80. Ray-Chaudhuri, S.P., and A. Huga. Supernumerary chromosomes in two populations of the grasshopper, Aiolopus Sp. B. and their behavior during spermatogenesis. Jour. Genet. 53:363-378, 1955.

81. Roman, H. Mitotic non-disjunction in the case of interchanges involving the B-type chromosome in maize. Genetics 32:391-409, 1947.

82. Roman, H. Directed fertilization in maize. Proc. Nat. Acad. Sci. 34:36-42, 1948.

83. Roman, H. Factors affecting mitotic non-disjunction in maize. Genetics 35:132-133, 1950.

84. Rütishauser, A. Genetics of fragment chromosomes in Trillium grandiflorum. Heredity 10:195-204, 1956.

85. Samejema, J. Meiotic behavior of accessory chromosomes and their distribution in natural populations of Lilium medeoloides A. Gray. Cytologia 23:159-171, 1958.

86. Sarvella, P. The behavior of accessory chromosomes in tetraploid rye. Hereditas 45:505-563, 1959.

87. Schertz, K.F., and R.P. Murphy. Fertility in relation to chromosome constitution and behavior in Bromus inermis Leyss. Agron. Jour. 50:372-376, 1958.

88. Sigurbjornsson, B., A. Mochizuki, and J.D. Truscott. Studies on the cytology of bromegrass, Bromus inermis Lyss. Can. Jour. Pl. Sci. 38:111-117, 1958.

89. Snedecor, G.W. Statistical methods. The Iowa State College Press, Ames, Iowa, 1946.

90. Sparrow, A.H., and V. Pond. Supernumerary chromosomes in diploid and triploid Trillium erectum L. Genetics 35:694, 1950.

91. Sparrow, A.H., V. Pond, and R.C. Sparrow. Distribution and behavior of supernumerary chromosomes during microsporogenesis in a population of Trillium erectum L. Am. Naturalist 86:277-292, 1952.

92. Sprague, G.T. Corn and corn improvement. Academic Press Inc. New York, N.Y. 1955.

93. White, M.J.D. Cytogenetics of Orthopteroid insects. Adv. Genet. 4:267-330, 1951.

94. Witkus, E.R., T.J. Lowerey, and C.A. Berger. The cytology of Xanthisma texanum D.C. II Additional chromosome types. Bull. Torrey Bot. Club 83:367-376, 1955.

95. Wylie, A.P. The history of the garden narcissi. Heredity 6:137-156, 1952.

A P P E N D I C E S

APPENDIX A

Analyses of fertility data for S-841, test 2

Table I: Analysis of variance and variance components of fertility in S-841 parents of test 2.

Source	Degrees of Freedom	Mean Square	Components of Variance	Variance in percent of Total
Total	179	90.33	90.05	100.0
Chromosome groups	3	41.85	- 6.66	- 7.4
Parents within groups	14	638.38**	54.31	60.3
Clones within parents	72	66.14**	23.44	26.0
Spikes within clones	90	18.96	18.96	21.1

k = 2 k3 = 178/179 r2 = 170/179
k1 = 2 r = 10 s = 61.67
k2 = 2 r1 = 10 s1 = 123.34/179

Table II: Analysis of variance and variance components of fertility in open-pollination progenies of S-841 in test 2.

Source	Degrees of Freedom	Mean Square	Components of Variance	Variance in percent of Total
Total	779	229.19	229.19	100.0
Chromosome groups	3	1204.85	.66	.3
Progenies within groups	22	1031.96**	20.64	9.0
Plants within progenies	364	388.76**	180.39	78.7
Spikes within plants	390	27.50	27.50	12.0

k = 2 k3 = 778/779 r2 = 750/779
k1 = 2 r = 30 s = 172.31
k2 = 2 r1 = 30 s1 = 516.93/779

APPENDIX B

Analysis of fertility data for S-1333, test 1 and test 2

Table I: Analysis of variance and variance components of fertility in S-1333 parents of tests 1 and 2.

Source	Degrees of Freedom	Mean Square	Components of Variance	Variance in percent of Total
Total	139	92.51	93.70	100.0
Chromosome groups	2	1807.79	18.06	19.3
Parents within groups	11	552.99**	48.10	51.3
Clones within parents	56	38.62**	10.92	11.7
Spikes within clones	60	16.62	16.62	17.7

k = 2	k3 = 138/139	r2 = 130/139
k1 = 2	r = 10	s = 40.71
k2 = 2	r1 = 10	s1 = 81.43/139

Table II: Analysis of variance and variance components of fertility in open-pollination progenies of S-1333 in tests 1 and 2.

Source	Degrees of Freedom	Mean Square	Components of Variance	Variance in percent of Total
Total	539	237.40	237.43	100.0
Chromosome groups	2	1097.12	.53	.2
Progenies within groups	15	969.51*	17.53	7.4
Plants within progenies	252	413.11**	193.02	81.3
Spikes within plants	270	26.35	26.35	11.1

k = 2	k3 = 538/539	r2 = 510/539
k1 = 2	r = 30	s = 102.22
k2 = 2	r1 = 30	s1 = 381.50/539

APPENDIX C

Analysis of fertility data for Summit selections, tests 3 and 5

Table I: Analysis of variance and variance components for fertility in selected Summit parents, test 5.

Source	Degrees of Freedom	Mean Square	Components of Variance	Variance in percent of Total
Total	197	91.68	91.67	100.0
Chromosome groups	3	122.13	- 2.80	- 3.1
Parents within groups	29	306.62**	36.66	40.0
Clones within parents	66	80.88**	22.82	24.9
Spikes within clones	99	34.99	34.99	38.2

k = 2	k3 = 196/197	r2 = 192/197
k1 = 2	r = 6	s = 46.54
k2 = 2	r1 = 6	s1 = 139.64/197

Table II: Analysis of variance and variance components of fertility in open-pollination progenies of selected Summit plants, test 3.

Source	Degrees of Freedom	Mean Square	Components of Variance	Variance in percent of Total
Total	989	236.41	236.41	100.0
Chromosome groups	3	957.36	- 1.60	- .7
Progenies within groups	29	1488.00**	36.07	15.3
Plants within progenies	462	373.17**	170.86	72.3
Spikes within plants	495	31.08	31.08	13.1

k = 2	k3 = 988/989	r2 = 960/989
k1 = 2	r = 30	s = 232.7
k2 = 2	r1 = 30	s1 = 698.19/989

APPENDIX D

Tests of significance of progeny-parent regressions for fertility

Table I: Tests of significance for differences between group regressions.

Groups		D.F.	Sums of squares and products Sx^2	Sxy	Sy^2	Regression coefficients	Errors of Estimate SS*	D.F.
1. Tests 1 & 2:	1	18	60892.33	50955.46	43220.16	.4301	580.00	17
	2	16	45440.87	39507.79	35229.27	.2911	879.90	15
	3	15	45615.62	39106.85	34325.29	.0872	798.50	14
	4	6	15611.71	15077.49	14919.19	.1658	357.64	5
	Sums	55	167560.53	144647.59	127693.91		2616.04	51
Average regression		59	167560.53	144647.59	127693.91	.2463	2826.05	54
2. Test 3:	1	9	22797.11	19023.02	16169.27	.3327	295.54	8
	2	12	31607.72	25287.50	20639.68	.6698	408.63	11
	3	5	14102.09	11223.79	8963.21	.7940	30.25	4
	4	3	8090.01	6323.89	5060.66	.3156	117.39	2
	Sums	29	76596.93	61858.20	50832.82		851.81	25
Average regression		32	76596.93	61858.20	50832.82	.5304	877.34	28

* $Sy^2 - (Sxy)^2/Sx^2$

Table II: Analysis of variance.

Source	Tests 1 & 2			Test 3		
	DF	SS	MS	DF	SS	MS
Deviation from average regression	54	2826.05		28	877.34	
Deviation from individual group regr.	51	2616.04	51.29	25	851.81	34.07
Differences among group regressions	3	210.01	70.00	3	25.53	8.51
F.		1.36 n.s.			.24 n.s.	