GENETIC STUDIES OF COMMON WHEAT USING
THE TECHNIQUE OF MONOSOMIC ANALYSIS

by

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TABLE OF CONTENTS

INTRODUCTION

A relatively new method has been devised for studying the inheritance of Mendelian factors in polyploid species of plants. It aptly is termed the monosomic method of analysis, for it involves the breeding of monosomic plants. Such a plant is deficient for an entire chromosome of a homologous pair; i.e., its sporophytic chromosome complement is 2n-1. The unpaired chromosome is called a monosome. A monosome may be traced from one generation to the next, and genetic consequences accompanying the monosome are ascribed to genes which it carries.

The use of monosomics may lead to new genetic information which is of practical value to the plant breeder. In addition, they may be used by the breeder to transfer intact an entire chromosome to a specific variety from another variety, or even from a related species.

Investigations utilizing monosomic types available in common wheat, _Triticum_ _vulgare_ Vill., were initiated at Kansas State College in 1947. It is the purpose of this thesis to review literature pertaining to monosomics or otherwise related to the problems encountered; and to report experimental results accruing from the studies thus far completed.

REVIEW OF LITERATURE

Occurrence of Monosomics

The occurrence of monosomic individuals frequently has been

mentioned in the literature. Blakeslee and Belling (5) in 1924 reported finding two plants of jimson weed, (a diploid, 2n=24), with monosomic branches. N-1 gametes produced on the branches did not function. McClintock reported a similar occurrence in diploid corn, 2n=20, (22). Root tissue displayed 20 chromosomes, but microsporocytes had nine bivalents and one univalent, $(9_{II} - 1_I)$. The plant was very weak and died before producing pollen.

Bridges (6) in 1921 studied a deficiency for the fourth linkage group in Drosophila. He traced the origin of the condition to nondisjunction of the fourth chromosome during meiotic division. Apparently deficient gametes are viable in Drosophila, for the deficiency was transmitted. The explanation may be that in animals there is no growth of haploid tissue comparable to the gametophytic generation in plants. Bridges pointed out that the phenomenon enables positive identification of a chromosome with the carriage of genetic factors; and that the advantages of sex linkage in the study of genetic relations are extended to an autosome.

Clausen and Cameron in 1944 (11) summarized nearly 20 years of work with monosomics in Nicotiana tabacum, an allotetraploid with 2n=48. According to them, the first two monosomic types in N. tabacum were reported by Clausen and Goodspeed in 1926. One of the monosomes was associated with transmission of a basic flower color in tobacco. Since that time, additional monosomic types have been isolated in N. tabacum by various means so that the set of 24 possible monosomics in that species is considered complete. By the use of these different monosomics in various

crossing procedures, 18 genes have been located on nine chromo-
somes. The work with monosomics in tobacco has led to consider-
able clarification of interspecific relationships within the
genus and to the probable origin of polyploid tobacco from basic
diploid species (9). Nullisomics, (2n minus a homologous pair),
have not been obtained in tobacco. The occurrence of such in-
dividuals is apparently limited to still higher polyploid forms
(18). Clausen (9) presents evidence that certain genes are not
present in N. tabacum which are found in one or the other of the
parent diploid species. Presumably those genes have been lost
since the origin of tabacum. If such loss of genes has been gen-
eral, it might explain the inviability of a sporophyte without
each chromosome represented at least once.

In common wheat aberrant types known as speltoids, from
their resemblance to Triticum spelta L., commonly occur. Spel-
toidy has been the subject of a number of investigations, both
cytological and genetic. Nilsson-Ehle, according to Huskins (15),
found such types as early as 1904. In following years he stud-
ied their genetic behavior in considerable detail. According to
the breeding behavior of speltoids, they were grouped into clas-
ses A, B, and C. Huskins (14, 15) demonstrated that B-type spel-
toids are due to a simple monosomic relationship. The absence of
a single chromosome, (later designated chromosome IX by Sears,
31), causes a heterozygous speltoid condition. Such a plant pro-
duces normals and monosomics in about the ratio of 1:5, along
with a very few nullisomics, (homozygous speltoids). Huskins
concluded also that A-type speltoids are due to an undetectable

chromosome deficiency; and that the C-type is due to a detactable
deficiency in the same chromosome. Each type has a characteris-
tic breeding behavior. Types A and C, with less drastic defi-
ciencies, produce more homozygous speltoids than Type B.

Fatuoidy in hexaploid oats is directly comparable to spel-
toidy in hexaploid wheat (13). Fatuoids resemble the wild oat,
Avena fatua L.

Kihara (1924) and Nishiyama (1928) both worked with two
different monosomics in common wheat according to Lammerts (18)
and Sears (29). Corresponding nullisomics were obtained by self-
ing. By crossing the two monosomics, a few very weak "double
nullisomics" were obtained with only 19_{II} instead of the normal
21.

Love (19) in 1938 reported the occurrence of a white-chaff
variant in a golden-chaff variety of common wheat. This was
traced to the loss of one arm from a chromosome. In the hetero-
zygous condition, one bivalent consisted of a long and a short
chromosome.

Love (21), Powers (28), and Semeniuk (35) have also reported
appearance of monosomic plants in Triticum vulgare. Their work,
however, was concerned with meiotic behavior in such aberrant
plants, and not in genetic studies through their use.

Sears (29) obtained 11 aberrant wheat plants in the variety
Chinese Spring (also known as Chinese, C.I. 6223) by pollinating
a haploid with normal pollen. Five of the group were simple mon-
osomics; the remainder had various combinations of bivalents, un-
ivalents, trivalents, and rings of four during meiosis. Sixteen

univalents were observed in the 11 plants. From these plants Sears (30) reported in 1941 that he had obtained seven different monosomics and their corresponding nullisomics. Five of these were found to involve chromosomes present in the Emmer or tetraploid wheat group (2n=28). They were numbered I through V. Two of the monosomes belonged to the additional genom present in hexaploid wheat (2n=42) and were numbered XV and XVI. Additional monosomics were obtained by various means so that the set of 21 possible types is complete except for monosomics XIII and XIV. Seventeen different nullisomics have also been obtained (31). Many of the nullisomics are nearly sterile. Some are completely male- or female-sterile. Most of the monosomics do not differ appreciably from normal Chinese wheat.

Cytological Behavior of Monosomics

A number of investigators have studied meiotic behavior in aneuploid plants including simple monosomics (25, 28, and 40). The apparently normal behavior of a monosome, according to their observations, is summarized as follows. At first metaphase (M_I), it is observable as a univalent, frequently lying some distance off the metaphase plate. As the bivalents disjoin, one group to each pole, the univalent may migrate to the plate and divide late. In this case the daughter chromatids move to the poles where they may or may not arrive in time to be included in the daughter nuclei. Or the univalent may fail to divide at first division. In this event it may be included in one of the daughter nuclei if its chance position in the cell allows. During

second division univalent chromosomes which did not divide previously proceed to divide normally, or they may be seen to lag at the plate. The daughter chromatids resulting from a monosome previously divided are incapable of redivision and lie at random in the cell. They may be incorporated in a daughter nucleus. A chromosome not included in a new nucleus at either division forms a micronucleus. From such behavior it should be a simple matter to distinguish monosomic from normal plants by studying microsporocyte divisions.

Several investigators have reported deviations from the described behavior of monosomics. Love (20) studied a plant with 41 somatic chromosomes which consistently displayed 11_{II} and 8_{I} in dividing microsporocytes. He considered that an atypical mitosis had occurred, producing one daughter cell with 11 chromosomes, which was eliminated; and the other daughter cell with 30 chromosomes gave rise to the microsporocytes studied. Other instances were cited in which one or a few chromosomes were lost prior to meiosis. Love (21) found certain monosomics which had more than one univalent at M_I; and in some cases a trivalent was found, but no univalents. Powers (28) noted considerable meiotic instability in 42 chromosome wheat, particularly in hybrid material. Univalents were commonly found due to nonconjunction. It is considered that meiotic instability is inherited, and that it may be due to incompatible genes brought together in a hybrid (20, 24, and 35). Clausen and Cameron (11) reported frequent nonconjunction in tobacco, which gave rise to a specific monosomic type. He also mentioned that, in the various monosomic

stocks, aberrant divisions and aberrant progeny were common. Sears did not refer to irregular appearance of univalents in the Chinese material except in crosses with nullisomic III, which is partially asynaptic (31). He did report that univalents occasionally mis-divide and give rise to telocentrics and isochromosomes which appear much the same as monosomes.

Utility in Genetic Studies

Clausen (10) states that monosomic analysis is not only simpler, but also more precise than normal analytical procedure. Although it can be adapted to relatively complex situations such as the location of complementary, duplicate, and modifying genes, its simplest use is in assigning single genes to a particular chromosome.

Unusual factor segregation in hybrids derived from a monosomic parent are due to the breeding behavior of monosomics. Because of the frequent loss of monosomes during meiosis, 2n-1 plants produce a preponderance of n-1 gametes. Sears (31) found gamete production to be in the ratio of three deficient to one normal. He found further that deficient pollen in competition with normal pollen is functional only 1 to 15 percent of the time, averaging about 4 percent. These transmission rates are used in the following examples, which illustrate how a gene is traced back to a specific chromosome of a tested parent.

Parents	Monosomic tester of a standard variety	Tested variety
Constitution	$40 + A$ (or 20_{II} & 1_I)	$40 + aa$ (or 21_{II})
Gametes	$1 (20 + A) : 3(20)$	$20 + a$
F_1 types	1 normal, $(40 + Aa)$: 3 monosomics, $(40 + a)$	

It is apparent that an F_1 plant which is monosomic derives its unpaired chromosome from the normal parent; and that the recessive gene "a" is expressed only in monosomic F_1's in the absence of the dominant allele. It follows that crossing all 21 testers of the standard variety with a second variety should reveal in one generation all the simple recessive genes in the tested variety. That such procedure has so far given disappointing results may be due to a scarcity of simple recessive genes in the material tested (11). Another complicating feature is the common occurrence in polyploids of duplicate genes, complementary factors, and other gene complexes which may serve to mask recessive genes.

Dominant genes are located by the following procedure:

Parents	Monosomic tester of a standard variety	Tested variety
Constitution	$40 + a$	$40 + AA$
Gametes	$1(20 + a) : 3(20)$	$20 + A$
F_1 types	1 normal, $(40 + Aa)$: 3 monosomics, $(40 + A)$	

Normal F_1's are discarded, monosomics are selfed, and show the
following behavior:

Male gametes

	$(20 + A)$ 96% functional	(20) 4% functional
$(20 + A)$ 25% functional	$24\ (40 + AA)$	$1\ (40 + A)$
(20) 75% functional	$72\ (40 + A)$	$3\ (40)$

(left side label: Female gametes)

An F_2 ratio approximating 30 dominants to one recessive (97
"A" to 3 lacking "A") indicates that the dominant gene accompan-
ies the monosome under consideration. In a cross with any par-
ticular monosomic tester, a simple dominant factor segregates in
the normal 3:1 fashion in F_2 if it is not located on the unpaired
chromosome.

Procedures for analyzing duplicate genes and other gene com-
binations could be illustrated by simple modifications in the ex-
amples given.

Through the use of monosomics and nullisomics in various
crossing procedures, a number of genes have been located in var-
ieties of Triticum vulgare. Sears (31) reports the following in
Chinese wheat: the gene b_1 on chromosome IX slightly suppresses
awn development, but less actively than its allele B_1; other

genes on chromosome IX are responsible for suppression of spel-
toidy, for squareheadedness, and for pubescent nodes; on chromo-
some VIII is the hooded factor, Hd, which shortens and recurves
awns; X carries an active awn suppressing gene, B_2; XVI has a
gene for red seeds and a dominant allele to the sphaerococcum
gene which causes short culms, dense spikes, and small spherical
grains; chromosomes II and XX evidently carry weak factors pro-
moting awn length; and III carries genes essential to normal sy-
napsis. According to Sears and Rodenhiser (34), the variety Tim-
stein has two dominant, complementary genes for resistance to
stem rust race 56 on chromosome X. O'Mara (26) reports that Mar-
quis carries a strong awn inhibitor, B_1, on chromosome IX. Un-
rau (39) reported awn suppressors (B_1) on chromosome IX in Hymar
and Federation 41, and that chromosome X in those varieties does
not suppress awns. He found in Federation 41 a gene for red
chaff on chromosome I and susceptibility to leaf rust on chromo-
some IV. In Hymar, the clubhead gene was located on XX and one
of two genes for winter habit on IX.

Related Genetic Studies

Leaf Rust Resistance. The reaction of many wheat varieties
to leaf rust, caused by Puccinia triticina Eriks., has been stud-
ied and reported (17). That resistance to leaf rust is heritable
is commonly realized. Pawnee undoubtedly inherited the leaf rust
resistance of its Kawvale parent (8). Both varieties are highly
resistant to physiologic race 9 in seedling stages, while Paw-
nee's other parent, Tenmarq, is susceptible. The manner of in-

heritance of resistance to a particular race or group of races of leaf rust has not been widely studied.

Mains et al. in 1926 (23) reported that, in the cross Ful- caster x Kanred, the seedling resistance of Fulcaster to race 9 appeared due to a single incompletely dominant factor. Caldwell and Compton (7) reported in 1947 that resistance of Wabash to races 9, 31, 65, 78, 79, 101, and 110 appeared to be due to a single recessive factor in crosses with susceptible Michigan Am- ber. Penny (27) found in the cross Pawnee x Red Chief that re- sistance of Pawnee to race 9 was explained by a single incom- pletely dominant factor. Working with field resistance, where several different races were known to be present, Swenson et al. found resistant progeny in a cross of two susceptible varieties, Thatcher and Triunfo (37). Resistance seemed to depend on two complementary dominant genes, one from each parent.

Loose Smut Resistance. Inheritance of resistance to the loose smut organism, Ustilago tritici (Pers.) Rostr., has been sparingly studied although the reaction of many varieties to loose smut is known (1). In a review of disease resistance in 1943, Ausemus (2) cites several cases in which resistance seemed due to a single recessive factor. Other studies indicated great- er complexity. Tingey and Tolman (38) explained the field re- sistance of Hope wheat on the basis of three dominant additive factors. They worked with other varieties which apparently had two, one, and none of the resistance factors. Bever (4) reported 11 different physiologic races of U. tritici, and it appears that resistance to different races may be due to different factors.

Work on the inheritance of the smut resistance of Pawnee wheat
has not been reported.

Winterhardiness. The ability of a wheat variety to with-
stand cold winter temperatures has been shown in a number of in-
stances to be inherited in a complex manner. Hayes and Aamodt
(12) reported crosses between Marquis (spring) and Minhardi (win-
ter) wheat. They concluded that winter growth habit was closely
but not completely correlated with winterhardiness; and that,
therefore, winterhardiness must depend primarily upon cold re-
sistance. That habit and hardiness may be inherited independent-
ly was indicated by the appearance of segregates which would head
when spring planted, yet would withstand winter temperature.
However, cold resistance alone has been reported in a number of
instances to be very complex in its inheritance (3).

Inheritance of Awns. Watkins and Ellerton (41) reviewed
much of the literature pertaining to awn inheritance in wheat and
presented results of considerable study of awnedness in several
wheat species. According to them, full awn expression requires
the presence of at least three recessive genes. The presence of
one or more of the inhibiting alleles explains most of the cases
of awnletted and other partially awned wheats. As previously
pointed out, these three main awn genes are located on chromo-
somes VIII, IX, and X of Chinese and other wheats studied by use
of monosomic analysis. Watkins and Ellerton admit the probable
existence of minor modifying genes. They state that the sphaero-
coccum gene (or closely linked group of genes) also causes a
marked reduction in awn length. Sears (32), in reporting the lo-

cation of the sphaerococcum gene s on chromosome XVI, does not
mention an effect of the gene upon awn length of segregates from
the cross Chinese x Triticum sphaerococcum. It therefore seems
possible that Chinese and T. sphaerococcum do not differ with re-
spect to the awn gene in the sphaerococcum linkage complex. The
review of Watkins and Ellerton permits ready explanation of the
many cases of one to four gene differences with respect to awns
reported in the literature (3).

Seed Color. According to Sears (33), Nilsson-Ehle in 1911
showed that three additive, partially dominant factors were re-
sponsible for the various degrees of red kernel color found in
wheat. Many workers since have reported one, two, and three fac-
tor difference in varietal crosses (3). Penny (27) obtained a
trihybrid ratio in progeny of Pawnee x Red Chief. He assumed
that Pawnee had one gene, R_1, and that Red Chief had R_2 and R_3.
The assumption has been verified in unpublished work at Kansas
State College. Sears (31) demonstrated that Chinese has a single
factor for red seed on chromosome XVI, since nullisomic XVI
proved to be white-seeded.

MATERIALS AND METHODS

Seed of 19 different monosomics and two nullisomics in the
variety Chinese Spring wheat was obtained from Dr. E. R. Sears[1]

and planted in the Kansas State College greenhouse in the spring
of 1947. The plants were transferred to the nursery and used as
female parents in crosses with the variety Pawnee, C.I.11669.
Crosses were successful with monosomics I, III through XII, XV
through XVIII and XXI, and with the nullisomics I and VII. The
F_1 populations were grown in the greenhouse the following winter.
Seed from selected F_1 plants was sown in both the greenhouse and
field in the fall of 1948 to permit observations in F_2 populations.

For convenience the different F_1 populations will be spoken
of as crosses, each one identified by the number of the single
chromosome in the Chinese parent. F_1 plants were grown in indi-
vidually numbered 5-inch clay pots. A specific F_1 plant will be
referred to by both cross and pot number, as VI-345. The F_2's
from such a plant will be termed family VI-345.

Cytological Procedures

Cytological studies of the parent material were not made.
Instead, crosses were attempted with two different Chinese parents
of each type in order to increase the chance of using at least one
that was monosomic. It was planned to study F_1 plants cytologi-
cally to identify a sufficient number of monosomic F_1 plants for
the investigations. Due to inexperience most of the spikes col-
lected from F_1 plants and preserved for study were found to be
too immature to show meiotic divisions. This necessitated the
study of plants in a number of F_2 families to determine whether
or not the F_1 parent had been monosomic.

Spikes were collected and fixed in Carnoy's fluid for two

days, then transferred to 70 percent alcohol. Anther smears were
prepared using the acetocarmine method (36). Plants were con-
sidered monosomic if a number of microsporocytes showed indica-
tions of a univalent of M_I or later division stages. In three
cases, chromosome counts were made at diakinesis or early ana-
phase$_I$. Many observations were made without cover slips. Some
slides were kept temporarily with paraffin-gum mastic seal. Se-
lected smears were mounted in balsam after immersion for about
five minutes in each of the following solutions: 10 percent ace-
tic acid; absolute alcohol-glacial acetic 1:1, 3:1, and 9:1; 100
percent alcohol; and alcohol-xylene 7:3.

Rust Experiment

Reaction to race 9 of leaf rust was determined in the green-
house for the Pawnee and Chinese parents, all F_1 plants and selec-
ted families of F_2 plants. Pure race cultures of urediospores
were propagated on seedling of Cheyenne, C.I. 8885, and used as
inoculum. Purity was insured by periodic testing upon differen-
tial host varieties.

Pawnee and F_1 seedlings were inoculated by injecting aqueous
spore suspension through the leaf curl with a hypodermic syringe.
Readings were made on infected leaves about ten days later.

Reaction of F_2 families and of the Chinese parents was deter-
mined by growing the various stocks in pots (25 seedlings in a
4-inch pot or 35 in a 5-inch pot), and inoculating by thoroughly
dusting urediospores over the seedlings. Seedlings were sprayed
with a fine water mist before inoculation and were kept in a

moist chamber for 24 hours after. Rust readings were made 10-12 days after inoculation. The reading was taken from the primary leaf when possible; but in many plants of intermediate or "X" type reaction it was necessary to resort to the second seedling leaf to determine the reaction. Rust readings were made in accordance with the scale illustrated by Johnston and Mains in 1932 (16).

Loose Smut Experiment

Selfed progeny of all parent plants and a representative selection of F_1 plants were inoculated with race 1 of loose smut in the greenhouse in the spring of 1948. Plants of Red Chief, Clarkan, and Timstein were also inoculated to serve as inoculum check varieties. Resulting seed was planted in the greenhouse in the fall of 1948. Nine hundred plants were grown in an 8 x 16 foot floor bed. The bed accommodated 36 F_2 families and corresponding Chinese parent plants spaced 3 x 6 inches. Remaining seed of Chinese, Pawnee, Red Chief, Clarkan, and Timstein was grown, four or five plants to an 8-inch clay pot. Winter varieties were placed outdoors for a vernalization period of 45 days and returned to the greenhouse.

Inoculation was accomplished by injecting aqueous chlamydospore suspension into each primary and secondary floret with needle and bulb. A few basal and terminal spikelets were first removed, and the spikes were left covered with glassine bags to improve humidity conditions. Central florets were not removed, nor were they harvested. Inoculations were made on the second

day of blooming, or when anthers in about the central half of the spike were extruded.

Winterhardiness Test

Eight-foot space-planted rows of F_2 families and parental checks were sown in the field in the fall of 1948 to permit observations on winter survival. Three rows from each of 15 crosses were grown. Pawnee was planted in every fourth row, and eight rows of various Chinese types were included in a block.

EXPERIMENTAL RESULTS AND DISCUSSION

Cytological Observations

Through studying anther smears of F_1 plants, nine plants from as many crosses were analyzed as monosomics. Strong evidence of a univalent at M_I, as illustrated in Fig. 1, was often the basis for classifying a plant monosomic. F_1 progeny of Chinese nullisomics I and VII were considered monosomic from the nature of the cross. From anther smears of their F_2 progeny, an additional 28 F_1 plants were found to be monosomic. The combined data indicated monosomic plants in all of the fifteen crosses. In several cases when an F_1 population was found to be heterogeneous, sibs of a given phenotype were presumed to be monosomic when one was so classified cytologically.

In the case of cross VIII, phenotypic and cytological data did not agree. Since Chinese chromosome VIII carries the dominant gene Hd (31), monosomic F_1's lacking that chromosome should
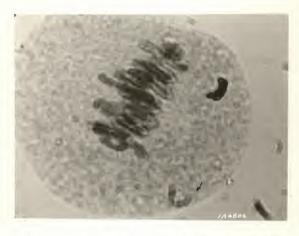
Fig. 1. Photomicrograph of a single microsporocyte at metaphase of the first meiotic division. The isolated univalent is chromosome XII. The arrow at lower right indicates non-chromatin material. (Approximately 2800 x)

be hoodless. F_1 plants VIII-361 and -365 were classified cyto-
logically as monosomic, yet they were hooded. Whether the analy-
sis was in error or whether those plants displayed a univalent
other than chromosome VIII was not determined.

In several F_2 plants examined, more than one univalent was
found. In no case did the preparations permit the statement that
multiple univalents were a constant feature of a plant. One such
plant was a dwarf in the F_2 family III-297. Seven univalents
were observed in one PMC at first anaphase. Undoubtedly the
plant was a nullisomic III, which is reportedly asynaptic (31).
One of its sibs was apparently monosomic, but occasionally showed
two univalents at M_I.

In cross X, F_1 plants were easily classified as normal or
monosomic on the basis of awn length. Several presumably normal
F_2 plants from cross X showed two univalents. In one of these,
however, 21 bivalents were clearly seen in a PMC at diakinesis.
Several plants examined in the F_2 were presumably from monosomic
F_1's. One univalent seemed to be a constant feature, but occa-
sionally two univalents were found.

In crosses I, V, XI, and XV a limited number of F_2 plants
were studied which showed two univalents. In two of the cases a
single cell at early anaphase revealed 41 chromosomes. Adequate
evidence was not secured to permit an explanation of the appear-
ance of extra univalents in material which is assumed to be nor-
mal or monosomic. In view of rather scattered occurrence, it
seems probable that a reciprocal translocation is involved, which
might form rings of four in some cases and chains of three and a

univalent in other cases. No such configurations were observed, although they would be best seen at diakinesis, and that stage was little studied. It is also possible that some of the material is doubly monosomic. Fortunately, results to be reported are not contingent upon any of the crosses in which unexpected behavior was observed except cross X. In this case, awn suppression is believed to be a reliable indicator of the presence of Chinese chromosome X.

Leaf Rust Studies

The Pawnee parent exhibited high resistance to race 9 of leaf rust, giving usually a zero reaction with chlorotic fleck-ing, but an occasional very small pustule was found. The various Chinese types tested showed pustules of type 4 which were charac-teristically light colored. F_1 plants were variously read from zero to two-plus. This was often on the basis of one or a very few pustules resulting from the needle method of inoculation. No cross was outstanding with uniformly high or low readings. In general the F_1's were resistant, but less resistant than Paw-nee. Resistance of Pawnee thus appeared to be incompletely dom-inant.

The first group of F_2 plants to be tested included families from 16 crosses. Plants were grouped into three classes: those showing the high resistance of Pawnee; those with the 4 reaction of Chinese; and an intermediate group. The intermediates were of the X-type, showing both resistance and susceptibility in the same plant. The ratio of resistant type pustules to susceptible

type in the plants of this group varied considerably. In the
most resistant plants only one or a few pustules appeared at the
tip of the primary leaf. Resistance increased inversely with
the age of tissue, so that in these plants the second leaf was
highly resistant. At the other extreme in the X group were
plants showing resistant type pustules only from the center to
the base of the second leaf. Comprising the bulk of the group
were plants showing resistance on both leaves.

F_2 families of cross X seemed outstanding, giving 4 resis-
tant, 23 X-type and 4 susceptible plants. The latter four were
dwarfed and perhaps nullisomic. Totaling all other families gave
a ratio of 40:322:312, suggesting 1:8:7 with expected numbers of
42:337:295. The hypothesis was supported by a Chi-square value
of 1.81 giving a probability of 0.42.

A second test was run to gain additional data in cross X
and in certain other crosses where slight variations from the
1:8:7 hypothesis were apparent. On a two factor basis, the in-
termediate group should include three genotypes. An attempt was
made to classify X-type plants into three groups on the basis of
apparent resistance. Degrees of resistance were found to be con-
tinuous and intergrading so that definite classes could not be
established. Difficulty was also encountered in separating
plants with the Pawnee type of resistance from the most resis-
tant X-types, so that it was decided to group all plants with
any resistance against those with no resistance.

In the second test, certain plants of cross IV differed
significantly from the 9:7 ratio. Numbers in this cross were

increased in a third test, and no reason was found to suspect
that chromosome IV was associated with resistance. Total results
of the three tests are given in Table 1.

Table 1. Reaction of F_2 families in the crosses of Chinese mon-
osomics x Pawnee to race 9 of leaf rust.

Cross number	Resistant plants	Susceptible plants	Test of fit to a 9:7 ratio Chi-square	Probability
I	31	25	.018	.898
III	83	63	.021	.890
IV	155	119	.011	.920
V	58	37	.905	.355
VI	44	33	.026	.880
VII	36	34	.670	.430
VIII	47	39	.092	.766
IX	47	28	1.250	.268
X*	86	67	.102	.755
X**	119	16	55.640***	<.001
XI	83	69	.168	.654
XII	23	22	.477	.490
XV	80	57	.280	.647
XVI	68	62	.813	.384
XVII	17	15	.117	.737
XVIII	71	60	.226	.601
XXI	53	49	.771	.398
Total****	982	779	.148	.700
Sum of chi-squares, D/F=16			5.947	.99
Heterogeneity chi-square, D/F=15			5.799	.98

* Families in cross X from normal F_1 plants.
** Families in cross X from monosomic F_1 plants.
*** Highly significant chi-square, probability less than .001.
**** Data from X** were omitted in calculations of total chi-
square, sum of chi-squares, and the heterogeneity chi-
square.

From the data obtained, the hypothesis is advanced that re-
sistance to race 9 in Pawnee is due to two incompletely dominant
complementary genes, Lr_3 and Lr_4, and that Chinese possesses the

recessive alleles, lr_3 and lr_4. This hypothesis can account for the previously reported one factor difference between Pawnee and Red Chief (27) by assuming that Red Chief has the genes lr_3 and Lr_4.

The location of the resistance genes is less clear. Obviously chromosome X of Pawnee is associated with resistance. However, if chromosome X carries but one of the genes, a 3:1 ratio should have been obtained in progeny of F_1 monosomic X plants. The great majority of plants in this group would carry one resistance gene, but the complementary gene would be free to segregate in a 3:1 fashion so that the two could be expected together in about three-fourths of the plants. The observed ratio among 135 such plants was approximately $7\frac{1}{2}$:1.

Another explanation of the results assumes that the two genes are linked on chromosome X. To allow 9:7 ratios in the bulk of the F_2 progeny would require very close to 50 percent of crossing over. A second required assumption is that there is an unusually high pollination rate by gametes deficient for chromosome X. Adjusting the transmission rate of deficient pollen to 16 percent, expected F_2 results are illustrated in the following diagram.

Male gametes

	(20 + X) 84% functional	(20) 16% functional
(20 + X) 25% functional	21 (40 + XX)	4 (40 + X)
(20) 75% functional	63 (40 + X)	12 (40)

(Left side label: Female gametes)

Under this hypothesis the expected F_2 results in cross X would be 88 percent resistant to 12 percent susceptible; or 118.8:16.2 expected compared with 119:16 observed. The figure for deficient pollen transmission could be lowered to 10 percent and observed, and expected ratios would still be in reasonably good agreement.

Since cytological studies within cross X cannot be considered conclusive, a third explanation is offered. It is possible that two monosomes are involved in the cross, each from Pawnee and each carrying a resistant gene. In such a case, results similar to those obtained might occur.

In the light of present information it appears that chromosome X of Pawnee carries at least one of two partially dominant complementary genes responsible for resistance to race 9 of leaf rust.

Loose Smut Studies

At the beginning of the studies the reaction of Chinese to loose smut was unknown. If it proved to be susceptible, genes for the high smut resistance of Pawnee might be disclosed in a cross between the two varieties. Physiologic race 1 of loose smut was chosen for the experiment because of its relative importance in the United States.

Pawnee proved to maintain practical immunity to the race used under greenhouse conditions. Forty-two plants grown from inoculated seed showed no infection. Satisfactory inoculum and methods were indicated by 36 percent infection in 11 plants of Clarkan; 35 percent infection in 17 Red Chief plants; and 19 percent infection in 27 Timstein plants tested. Among 187 Chinese plants of the various parental types grown, only 11 plants or 5.9 percent were infected. In each of the 11 plants only the first spike was infected; additional tillers were healthy. Eight of the plants had partially smutted heads.

Tingey and Tolman (38) in similar work classified varieties with less than 10 percent infection as resistant. By this criterion both the Pawnee and Chinese parents were resistant, and the varieties Clarkan, Red Chief, and Timstein were susceptible to the race of smut used.

Percentage of smut infection in all F_2 families has not been determined. There is no indication that the F_2 population is more susceptible than Chinese. The F_2 data may permit a genetic

explanation of the slight susceptibility of Chinese, as compared
with Pawnee.

Winterhardiness Studies

A number of F_2 families were grown in the winter wheat nur-
sery in the hope that it might be learned which chromosomes of
Pawnee are responsible for winterhardiness. The data obtained
are given in Table 2.

The mean survival of Pawnee plants was 89.6 percent. Sur-
vival rate for the entire F_2 population was 69.4 percent. Such
high survival in a spring-winter cross is unusual, and can no
doubt be largely explained by mild winter conditions. One plant
out of about 200 Chinese seedlings which emerged in the fall
lived through the winter. Several volunteer oat plants in an
adjacent plot failed to winterkill, demonstrating the mildness
of the season.

An analysis of variance was run upon the F_2 data obtained,
and the results are given in Table 3.

Table 2. Winter survival of F_2 families in the crosses of Chinese monosomics x Pawnee.

F_1 parent	Nature of F_1 parent	Plants emerged	Percentage survival of families	of crosses
XVIII-473	Unknown	22	81.8	
XVIII-476	Unknown	26	92.3	86.3
XVIII-478	Unknown	25	84.0	
III-279	Monosomic	30	83.3	
III-296	Unknown	32	81.3	84.7
III-297	Unknown	10	70.0	
I-251	Monosomic	26	84.6	
I-253	Monosomic	19	94.2	83.3
I-263	Monosomic	21	71.4	
XXI-490	Monosomic	30	83.3	
XXI-494	Unknown	28	78.6	81.9
XXI-497	Monosomic	14	85.7	
XVI-465	Monosomic	16	75.0	
XVI-468	Unknown	27	77.8	76.1
XVI-469	Unknown	28	75.0	
XV-437	Monosomic	13	46.1	
XV-455	Unknown	30	83.3	76.1
XV-435	Monosomic	28	89.3	
XI-416	Monosomic	23	47.8	
XI-424	Unknown	28	82.1	71.8
XI-417	Unknown	27	81.5	
X-403	Monosomic	22	50.0	
X-407	Monosomic	26	80.8	70.8
X-394	Normal	24	79.2	
IX-385	Monosomic	27	62.9	
IX-388	Unknown	24	66.6	67.1
IX-380	Unknown	19	73.7	
VII-260	Monosomic	29	55.1	
VII-261	Monosomic	19	73.7	62.3
VII-356	Monosomic	29	62.1	
VIII-359	Monosomic	20	60.0	
VIII-365	Monosomic	29	58.6	61.8
VIII-369	Unknown	19	73.7	
XII-429	Monosomic	23	65.2	
XII-431	Monosomic	17	52.9	61.3
XII-433	Monosomic	22	63.6	
V-339	Monosomic	29	72.4	
V-321	Unknown	26	42.5	57.3
V-323	Unknown	27	55.5	
IV-315	Monosomic	22	40.9	
IV-307	Monosomic	21	52.4	56.3
IV-317	Unknown	28	71.4	
VI-345	Monosomic	31	45.2	
VI-346	Monosomic	23	43.5	47.6
VI-354	Monosomic	30	53.3	

Table 3. Analysis of variance of winter survival data summar-
ized in Table 2 for F_2 populations in 15 Chinese x
Pawnee crosses.

Factors	D/F	Estimated variance	F-value	Probability
Total	44	229.01		
Between crosses	14	395.62	2.615	1.714
Error	30	151.26		

The above analysis indicates that the observed difference in
winter survival between crosses would be obtained by chance alone
in about 1.7 percent of repeated trials if the crosses are all a-
like with respect to winterhardiness. Therefore, it is concluded
with considerable assurance that there is real difference between
crosses responsible for different degrees of winter survival.

The least significant difference between mean survival per-
centages of different crosses was calculated to be 20.5 percent.
This only permits the statement that those crosses with extremely
high survival rates are significantly different from crosses with
low survival rates. As can be seen from the final column of Ta-
ble 2, no cross or crosses were significantly higher or lower
than all others in percent of survival. Consequently no attempt
was made to conclude from the data obtained that any particular
chromosome tested is involved in raising or depressing the degree
of winterhardiness.

Awn Studies

Plates I, II, and III illustrate various F_1 awn types appear-

EXPLANATION OF PLATE I

Photographs of typical heads from crosses in which there was observed no heterogeneity of awn type in F_1. Each head is from a different Chinese monosomic x Pawnee cross.

Head a is from cross III; b from IV; c from V; d from VI; e from VII; f from XI; g from XII; and h is from cross XVIII.

PLATE I

a   b   c   d   e   f   g   h

EXPLANATION OF PLATE II

Photographed wheat heads from three Chinese x Pawnee
F_1 populations in which variation with respect to awn type
was apparent.

Heads a, b, and c are from cross VIII. Head a is a
typical Chinese head; b is hooded, from a normal F_1; and c
is hoodless, from a monosomic F_1.

Heads d and e are speltoid heads from cross IX, show-
ing variability in awn length.

Heads f and g illustrate the type of awns found in
normal and monosomic plants respectively in cross X.

PLATE II

EXPLANATION OF PLATE III

Photographed wheat heads from three Chinese x Pawnee
F1 populations which were heterogeneous with respect to awn
type.

Heads a, b, and c are from cross XV. Slight variabil-
ity in awn length is illustrated.

Heads d and e are from monosomic plants in cross XVI.
Both have short awns. Head e illustrates clavate head
shape.

Heads f and g illustrate the two awn types observed in
cross XXI in normal and monosomic plants respectively.

PLATE III

Col836

a　b　c　d　e　f　g

ing in most of the crosses of Pawnee x Chinese monosomics. Paw-
nee has long awns, the longest measuring about seven cm. Awn-
lets of the Chinese parent were found to be less than one cm. in
length, varying slightly in different stocks. The spikes in
Plate I are representative of crosses in which no variation in
awn length was found among the several F_1 plants of each cross.
With the exception of g on Plate I, heads pictured are probably
representative of the awn type which would be found in disomic
Chinese x Pawnee F_1's. The longest awnlets of such plants, found
in crosses I, III, IV, VI, VII, XI, and XVIII, ranged from about
one to two cm. in length. In those crosses there was apparently
no difference in awn length between monosomic and normal plants.

Heads a, b, and c in Plate II are from plants in cross VIII.
Spike a resulted from a self-pollination of Chinese, and is beard-
less. Spike b is from a normal F_1 plant, is hooded, and short
awned. Spike c is hoodless, has awns 4.5 cm. in length, and came
from a monosomic F_1. The differences among the three plants are
explained as follows: a carries the gene Hd; b has the genes Hd
hd; and c has only hd. This analysis is possible because it is
known that Chinese carries the dominant gene Hd, suppressing awns,
on chromosome VIII. Its absence in the monosomic F_1 indicates
that Pawnee has the recessive allele hd.

Absence of chromosome IX is responsible for speltoidy. Thus
monosomic F_1's of cross IX are easily distinguished. Considerable
variability in awn length was encountered in cross IX, even among
plants known to be monosomic. Plate II, heads d and e, display
such variability. Both heads are speltoid, but differ in awn

length by as much as two cm. Such variation was found among heads
of a single plant. No awn difference was apparent between normal
and monosomic plants in the cross. Consequently, Chinese and
Pawnee were assumed to have the same awn gene carried on chromo-
some IX, namely the recessive b_1.

Two awn types were found in cross X. Monosomic F_1's had
awns up to four cm. in length, while plants considered disomic
were awnletted. It seems apparent that the dominant awn inhibit-
ing gene B_2 on chromosome X of Chinese is responsible for the dif-
ference, which is illustrated on Plate II, f and g. B_2 is present
in normal F_1's, while the allele b_2 from Pawnee is alone in mono-
somics and awns are less inhibited.

All plants in cross XII had awns approximately 3.5 cm. in
length, as illustrated in Plate I g. Three plants were found to
be monosomic, and the two remaining F_1's were considered to be
monosomic also.

Some difference in awn length was apparent in different F_1
plants of cross XV. This is illustrated by a, b, and c on Plate
III. No significance could be attached to the matter, for one of
the short-awned plants was analyzed as monosomic.

F_1's in cross XVI were mostly long-awned, as illustrated in
d of Plate III. One long-awned plant was found to be monosomic.
The same is true of cross XXI. Long and short-awned plants of
the latter cross are compared in f and g on Plate III.

While the appearance of long-awned F_1's in crosses VIII and
X was not unexpected in view of the known awn suppressers in Chi-
nese, similar plants in crosses XII, XVI, and XXI are not so well

accounted for. One explanation would be that the latter plants are doubly monosomic, deficient either for chromosome VIII or X in addition to the expected deficiency. However, such an explanation is ruled out in every case. Deficiency for Chinese chromosome VIII would increase awn length, but also require hoodlessness. Lack of chromosome X should affect resistance to leaf rust. Awned plants in crosses XII, XVI, and XXI were not hoodless, nor were their F_2 families excessively resistant to leaf rust.

A working hypothesis is proposed to account for awn stimulation in monosomic F_1's lacking the Chinese chromosome XII, XVI, or XXI; and at the same time to account for the previously reported awn factors and their behavior. It has been well established that Chinese has two incompletely dominant, incompletely epistatic awn inhibitors, Hd and B_2. It has not been demonstrated that the recessive alleles, hd and b_2 stimulate awn development; but rather that, in the absence of Hd and B_2, awn development is permitted. Upon this basis a series of "A" genes is proposed. An "A" gene is (hypothetically) non-epistatic, but incompletely dominant over an awn producing allele a. A single recessive gene a in the homozygous condition aa could theoretically produce full awns if not inhibited by partially epistatic Hd or B_2. Assigning recessive a to chromosomes II and XX of Chinese, since it has been reported that they have an awn stimulating effect (31), and assigning similar genes to chromosomes XII, XVI, and XXI of Pawnee, resulting genotypes will be illustrated.

Chromosome	II	VIII	X	XII	XVI	XX	XXI
Chinese	a_1	Hd	B_2	A_2	A_3	a_4	A_5
Pawnee	a_1	hd	b_2	a_2	a_3	a_4	a_5

Chinese is awn tipped, according to this theory, because of in-
complete inhibition of a_1 and a_4 by the incompletely epistatic
genes Hd and B_2. Pawnee has no inhibitors, and is completely
awned. Since there is no evidence that the two varieties differ
with respect to a_1 and a_4, those genes will not be further con-
sidered. An F_1 with no deficiencies for any of the above chromo-
somes would have the constitution Hd hd B_2b_2 A_2a_2 A_3a_3 A_5a_5, and
would be longer awned than Chinese because of greater dosage of
a and smaller dosage of Hd and B_2. Monosomic VIII F_1's would be
still longer because of removal of inhibitor Hd, allowing more
awn expression from the heterozygous Aa factors. Constitution
would be hd B_2b_2 A_2a_2 A_3a_3 A_5a_5. An identical explanation would
apply in the case of B_2, absent in monosomic X F_1's. Monosomic
F_1 plants in crosses with Chinese monosomic XII would be Hd hd
B_2b_2 a_2 A_3a_3 A_5a_5. They would be longer awned because of removal
of A_2, allowing more complete expression of awn producing a_2.
Crosses XVI and XXI would be explained in exactly the same man-
ner.

The preceding awn theory may be modified considerably and
still retain its essential principles. It is believed that this
or some other multiple-gene theory is quite necessary to explain
the occurrence of awned types in so many different crosses with

monosomic stock. The one proposed is not a contradiction but rather an extension of previous ideas.

Seed Color

Chinese is known (31) to have a single dominant factor for red kernel color on chromosome XVI. Pawnee also is reported to have a single gene, R_1, for red seeds (27). If the two varieties have different R factors, two-factor segregation should appear in most of the F_2 families, 15 red to one white seeded. In the cross Chinese monosomic XVI x Pawnee, F_2 plants would not have the Chinese R gene, but three-fourths of them should receive a dominant R from Pawnee. The ratio in this cross should then be 3R:1W. On the other hand, if the two varieties have the same R gene, no segregation should appear in F_2 except in cross XVI where only nullisomics (about one out of 30 expected) should have white seed.

Working on the two-factor hypothesis, a number of F_2 plants from other than cross XVI were examined. At the .999 probability level, at least one white-seeded plant should be found among 108 individuals if expected in the ratio of 1:15. Such a population failed to disclose any white-seeded plants.

Further evidence against the two-factor hypothesis was found in F_2's of cross XVI. Forty-five plants in two families from monosomic F_1's included no plants with white seeds. These data rule out the possibility of a 3:1 ratio.

It is therefore concluded that both Pawnee and Chinese have the constitution R_1R_1 r_2r_2 r_3r_3, and that R is located on chromo-

some XVI. That no white-seeded nullisomic XVI plants were obtained among 45 F_2's of cross XVI is not surprising when only one out of 30 was expected.

Miscellaneous Observations

In the course of considerable handling of F_1 and F_2 material of the cross Chinese x Pawnee, a number of characteristics were noticed which undoubtedly have a genetic basis and which might profitably be studied. One such characteristic appeared in the F_2 families of monosomic X F_1's. Seedlings of this cross grown for rust inoculation often developed isolated brown bands across leaves above the mid-point. Such a condition was reported by Johnston and Mains (16) in seedlings of the variety Loros grown in the greenhouse. The peculiarity appeared in about one-half of the F_2 plants in families of only monosomic X F_1's. Such a family of seedlings is compared with a normal family in Fig. 2. Any sound genetic explanation of the phenomenon seems to require that F_1 plants in the same cross show the condition also, and such was not observed. Normal plants in affected families, as determined by the Pawnee type of leaf rust reaction, never developed such "scalded" areas, nor did all of the plants which must have been monosomic. It is entirely possible that its appearance depends both upon a specific genotype and a specific environment.

Genes responsible for clavate head shape, illustrated in e of Plate III, were not located. The character is incompletely dominant, and is characteristic of most of the Chinese parent strains. Expression in the heterozygous condition is often very

Fig. 2. Comparison of F₂ seedlings from the cross Chinese monosomic X times Pawnee. Seedlings in Pot 409 are from a monosomic F₁ plant, while those in Pot 401 are from a normal F₁.

slight. That fact introduced enough error into notes taken on mature F_1 plants that non-clavate plants were recorded in several crosses. In later analysis the non-clavate head shape could not be positively correlated with absence of a specific chromosome.

There was found to be extreme segregation for height in F_2 material. Limited data indicated height ranging from 29 to 54 inches in different F_2 plants under crowded greenhouse conditions. In the same material there was considerable range in number of tillers per plant, and in width and length of leaves. In the F_1 population there was indication that the tendency to produce supernumerary spikelets and supernumerary florets could be studied in the cross Chinese x Pawnee.

<center>SUMMARY</center>

Genetic and correlated cytological studies were made upon F_1 and F_2 populations resulting from crossing sixteen different monosomic types of Chinese wheat with the variety Pawnee. The chief characters studied were: resistance to race 9 of leaf rust; resistance to race 1 of loose smut; winter survival; awnedness; and inheritance of red kernel color.

Evidence is presented which indicates that Chinese and Pawnee differ with respect to resistance to race 9 of leaf rust by two incompletely dominant complementary genes for resistance in Pawnee; and that at least one of the genes is on chromosome X.

The variety Chinese was found to be resistant to race 1 of loose smut. In addition, the varieties Red Chief, Clarkan, and Timstein were found to be susceptible to the same race of smut.

Data were obtained under mild winter conditions showing a significant difference in winter survival of F_2 populations from different monosomic crosses.

F_1 observations indicated that chromosomes VIII, X, XII, XVI, and XXI of Pawnee are all involved in expression of awns. A working hypothesis is presented which can account adequately for such a number of awn factors and at the same time account for relatively simple genetic ratios commonly obtained.

It was concluded that Pawnee and Chinese possess the same gene, R_1, responsible for the expression of red kernel color. The gene is located on chromosome XVI.

Several additional characters which might be profitably studied in the same cross were observed and reported.

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