THE RELATIONSHIP OF CERTAIN MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERS TO STRUCTURAL ARRANGEMENTS IN TRITICUM VULGARE

Thesis for the Degree of Ph. D.

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David W. Gessford

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THESIS

This is to certify that the

thesis entitled

THE RELATIONSHIP OF CERTAIN
MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERS
TO STRUCTURAL ARRANGEMENTS IN TRITICUM VULGARE

presented by

DAVID WILLIAM GESSFORD

has been accepted towards fulfillment
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Everett H. Everson
Major professor

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THE RELATIONSHIP OF CERTAIN MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERS TO STRUCTURAL ARRANGEMENTS IN TRITICUM VULGARE

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David W. Gessford

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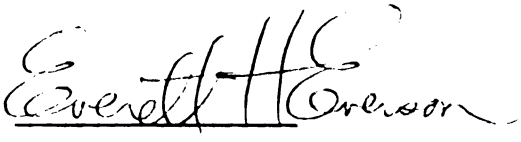
Approved 

THE RELATIONSHIP OF CERTAIN MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERS TO STRUCTURAL ARRANGEMENTS IN TRITICUM VULGARE

David W. Gessford

A cytological and genetical comparison was made between two red glumed mutant lines of wheat. The lines were Elliott's Translocation Stock and a red glumed Indian line C-591.

A mechanism for the origin of the light red chimera from Elliott's red glumed Translocation Stock has been proposed. This mechanism was based on the reversal of a position effect resulting from the original translocation(s) involved in the origin of the red glumed mutant line.

The genetics of glume color in the mutant and normal lines was studied. Glume color in Elliott's Translocation Stock was determined to be simply inherited with red incompletely dominant over white. The heterozygote was phenotypically distinguishable and classed as light red. No segregation for glume color was observed in crosses between red glumed varieties or between white glumed varieties. Therefore, glume color in the lines studied appeared to be controlled by the same locus.

The F_1 karyotypic analysis of the parents and hybrids involved in the study indicated no relationship between karyotypes and glume color. However, a large number of open pairs indicated a high level of structural heterozygosity in the hybrids studied.

Seedling rust tests on Elliott's Translocation Stock revealed that the X_4 plant in which the light red chimera occurred was heterozygous for rust reaction and that rust reaction and glume color were independently inherited.

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INTRODUCTION

Red glumes, as found in Triticum vulgare (common wheat) have been recorded in many of the species involved in its origin. Elliott (1957) reported the appearance of a red glumed plant in the F_2 of an irradiated cross of two varieties, neither of which had red glumes. The cross involved an Agropyron elongatum derivative. In addition to red glumes, the plant possessed most of the stem rust resistance of Agropyron elongatum, which was shown by Elliott to have been transferred by translocation.

The validity of the origin of the translocation as reported by Elliott (1957) had been questioned by certain wheat workers, who suggested that the resistance resembled that of Kenya Farmer and that it arose from outcrossing to Kenya Farmer.

This red glumed plant bred true for glume color until the X_4 generation when a light red chimera involving several tillers was found in one plant. Initial field observations at East Lansing, Michigan, indicated that progeny of this chimera were susceptible to stem rust in contrast to the resistance of the red glumed plants. Thus there seemed to be an association of stem rust resistance and glume color.

The occurrence of a red glumed mutant from a white glumed plant was reported in Indian wheat stocks by Swaminathan et al. (1959). The origin of this mutant, like that of Elliott's, was also associated with induced translocations. With the occurrence of these two red glumed mutants, it was then of academic interest to determine if the mutations were of a similar type, genetically and structurally.

This study was undertaken (1) to determine the inheritance of the glume character and the relationship of glume color and rust reaction in Elliott's radiation induced Translocation Stock; (2) to examine the allelism of glume color from the different mutant stocks; (3) to compare the karyotype of the chemical and X-ray induced translocation stocks by karyotypic analysis and (4) to attempt to clarify the immediate source of the rust resistance in Elliott's induced Translocation Stock.

REVIEW OF LITERATURE

MUTATIONS

Mutations are a major source of variability and their induction by either chemical mutagens, ionizing radiations, or radio-isotopes has occupied an important segment of research in recent years. Reviews by Gaul (1958), Smith (1958), Elliott (1958) and Muntzing (1961) deal with the history, theory and utilization of mutations. Recent work comparing chemical mutagens and ionizing radiations as to their efficiency and frequency as well as types of mutations they produce has been reported by Pal et al. (1958), Ehrenberg et al. (1961), MacKey (1962) and Nilan (1959).

GENETICS AND CYTOLOGY OF WHEAT

A great amount of literature has accumulated on the different phases of genetics and cytology of wheat. Very little, however, has been reported on the correlation between karyotype and genetic characters in hexaploid wheat. Much of the correlated genetical and cytological work in Triticum has dealt with inter species and generic hybrids and has been reviewed by Sears (1948).

Aase (1946) reviewed the effects of modifying environmental influences on pairing and other aspects of the cytology of cereals.

The chromosome segments in wheat are not completely homologous even between varieties, resulting in structural heterozygosity in hybrids, Thompson and Robertson (1930). Love (1941) reported that most and possibly all hybrids between vulgare wheats are heterozygous for one or more inversions. He indicated that all varieties of

tetraploid and hexaploid wheats might differ to a greater or lesser degree in arrangement of chromosome segments thus favoring conditions for deletions and other structural changes.

In 1951 Love presented data on varietal differences in the meiotic behavior of 19 Brazilian wheats and certain intervarietal combinations. The two types of abnormalities most prevalent were (1) failure of pairing resulting in lagging univalents and micronuclei in young pollen quartets and (2) lagging bivalents which usually resulted in disturbed meiosis while the lagging univalents did not have such an effect. No more than two or three pairs were involved in the chromosome irregularities in any one plant. There was a considerable range of meiotic irregularity in the varieties and hybrids studied.

Riley and Kimber (1961) examined the significance of meiotic irregularity on the structure of five wheat varieties in terms of their chromosome constitutions. The percent pollen mother cells with 2 univalents ranged from 4.2 - 8.2. Combined data for the five hexaploid varieties showed 6% irregular cells whereas meiosis in diploid ancestors resulted in 1.7% irregular cells with univalents. From the comparison of hexaploid and diploid pollen mother cells, the duplication of chromosomes had an effect on pairing.

Person (1956) pointed out that the level of meiotic irregularity, particularly pairing failure, was much higher in heterozygous material than in stable, more or less homozygous varieties. From the F_1 and through succeeding backcross generations, the return to the normal level of pairing accompanied the return to homozygosity.

Hollingshead (1932) studied variations of univalent frequency and found that in five varieties of wheat, 2.9 - 9.7% of the cells contained univalents while in hybrids between the varieties, 5.2 - 39.1% of the cells contained univalents. She compared genetic data with her cytological data and concluded that a high univalent frequency did not disturb the genetic ratios studied since certain chromosomes did not appear to be univalent more frequently than others.

Aase (1930) defines closed and open bivalents and while the closed type prevails, the "open" type occurs on an average frequency of little more than one per cell in T. vulgare and more frequently in certain hybrids.

GLUME COLOR INHERITANCE

Most workers, studying the inheritance of glume color, have reported that brown (red) glume color is dominant over white (yellow) glume color and controlled by a single factor. Ausemus (1946) in a summary of genetic studies in hexaploid and tetraploid wheats lists 22 authors who report monogenic inheritance and only two who report digenic inheritance.

Love (1938) and Sikka (1957, 1960A) report that the heterozygote is phenotypically indistinguishable from the homozygous dominant red parent but report a 1:2:1 segregation for the heterozygote in the F_2 which could only be distinguished by F_3 progeny tests.

Kajanus (Sears 1948) classified the glume color of wheat as black, red-brown, yellow-brown and yellow. Yellow was reported to be the multiple recessive type and color was controlled by three

independent factors, black differing from yellow by a single dominant gene. Red-brown and yellow-brown differed from yellow by a single dominant factor and both were hypostatic to black. He reported classification to be difficult.

Borojevic (1956) crossed a T. vulgare by a T. dicoccum variety, both of which were white glumed. The F1 was red glumed and segregated for 2 factors in the F_2 and later generations in a 9:7 ratio.

RUST GENETICS

The literature on inheritance of rust resistance is voluminous. Flor (1956), in his paper on complementary genic systems with flax, postulated that resistance of susceptibility in a variety depended upon the gene complement of rust reaction in the host variety and the gene complement for pathogenicity of the rust race interacting with the environment.

Person (1959) presented a model which diagramatically pictured separate genic systems of the host and the pathogen and their interaction to give the infection type seen on the plant.

Such gene for gene systems have also been found to be under genetic control and operating in barley and barley powdery mildew Moseman (1959), and wheat and wheat powdery mildew, Powers and Sando (1960).

The work of Loegering and Powers (1962) on the inheritance of pathogenicity in stem rust indicated that a gene for gene system was also operating between wheat and wheat stem rust. They found at least 8 independent genes for pathogenicity operating in Puccinia graminis F. sp. tritici.

Shebeski & Wu (1952) reported that the resistance from an Agropyron Triticum derivative in a cross with Apex, a susceptible variety, was dominant and governed by three complementary genes. Segregation ratios, however, were determined from instable populations with differing chromosome numbers.

TRANSFER OF RESISTANCE

For many years before the use of radiation for inducing mutations, there had been much interest in transferring disease resistance across species and genera. McFadden (Hunter and Leake 1933) incorporated the resistance of Yaroslov Emmer (T. dicoccum n=14) into T. vulgare (n=21) through crossing and repeated selection and Hayes et al. (1920) transferred rust resistance from T. durum (n=14) into T. vulgare (N=21) by a cross of varieties of the two species and repeated selection.

In more recent years there has been some success in transferring disease resistance across genera by inducing translocations in inter generic and intra species crosses.

Sears (1956) reported the transfer of leaf rust resistance from Aegilops umbellulata to wheat by the induction of a translocation. He first incorporated the Aegilops resistance into Triticum with a cross of Aegilops umbellulata (n=7) to Triticum dicoccoides (n=14). The T. dicoccoides (n=14) was then crossed with T. aestivum (n=21). The cross yielded plants with the whole wheat complement plus one Aegilops iso-chromosome. These possessed leaf rust resistance but also had undesirable growth characters. X-rays were then used to incorporate the Aegilops resistance into the wheat complement, by

means of a translocation, without the accompanying undesirable growth effects.

Elliott (1957) reported the transference of wheat stem rust from Agropyron elongatum to common hexaploid wheat (Triticum Vulgare) by means of irradiation. This method is presented in more detail in the materials and methods section.

Knott (1961) described three experiments in which radiation was successfully used to transfer rust resistance from an Agropyron chromosome to a wheat chromosome. He reported successful transfer of the rust resistance into the wheat chromosome in all three cases.

MATERIALS AND METHODS

Six lines of hexaploid wheat were used as parents in a diallel cross. The parent lines were a red glumed Translocation Stock, a white glumed Translocation Stock , C-591 red glumed, C-591 white glumed, Hard Federation (C.L. 4980) red glumed and Russell (C.I. 12484) white glumed. The red Translocation Stock was the red glumed line in which Elliott (1957) found the resistance from Agropyron elongatum transferred to a hexaploid, common wheat. Its parentage, as reported by Elliott (1957), included the cross of a tall wheatgrass (2n=70), Agropyron elongatum, to a hexaploid wheat by W. J. Sando in the 1930's. Stem rust resistance was stabilized at the octaploid (2n=56) level in the derivatives of the cross. Using the stem rust resistant octaploid as a female parent, it was crossed to the stem rust susceptible variety Idaed. The dry hybrid seeds were irradiated and one rust resistant, wheat-like, X_2 plant was found in an 18,000r X-ray population. The glumes of the resistant wheat-like plant were red, in contrast to the white glumes of both parents. The X_3 row from this red glumed, rust resistant X_2 plant was uniformly red glumed and rust resistant. No obvious segregation for glume color or other morphological characteristic was observed in the X_3, X_4 or X_5 progeny.

It was further reported that at least three multivalent associations were observed in the same cell of an F_1 hybrid (Translocation Stock x Idaed) indicating that possibly three interchanges were involved in differentiating the karyotype of the rust resistant stock from Idaed.

The white Translocation Stock was a white glumed line which came from a light red chimera found by F. C. Elliott in a red Translocation Stock plant being grown in a nursery at Brawley, California, in the X_4 generation. The chimera involved approximately one-half the plant. The seed from the light red chimera was grown for increase in the field at East Lansing, Michigan, for one generation then used as a parent line in this study.

The C-591 Red and C-591 White lines were obtained from M. S. Swaminathan of India. Pal et al. (1958) reported that "C-591 is highly stable, homogeneous and characterized by a fully bearded earhead, with white and pubescent glumes." Swaminathan et al. (1959) reported the origin of the C-591 Red line as follows: bread wheats were soaked for 24 hours in peanut, mustard and castor oils. In the F_2 generation, the peanut oil treated plants gave six mutant plants with red glumes. In two of the plants the red glumes were present only in some tillers, the other tillers having normal white glumes. The shade of the glume color was lighter in such chimeras than in mutants in which all tillers had red glumes. The C-591 Red line came from one of the red glumed mutant plants. They further reported that the mustard and peanut oil treatments gave dicentric bridges and acentric fragments indicating heterozygosity for inversions. Percentages of cells with laggards or bridge at anaphase I were 22-35%.

Hard Federation was a selection out of Federation in 1914 (Clark and Bayles, 1942) and has only T. vulgare in its pedigree.

Russell (Shands 1956) comes from a cross of Thatcher x (Illinois No. 1, W.38 x Hope selection). Hope is a selection from a cross

involving emmer (2n=28) and Thatcher is a selection out of a double cross involving a durum variety (2n=28) and vulgare varieties (2n=42). Therefore, Russell has T. durum and T. dicoccum and T. vulgare in its complex pedigree.

All plants used in this study were grown in a walk-in type growth chamber. Plants in the parental and F_1 generations were grown one to a pot while the F_2 generation was grown two plants to a pot. The light intensity was approximately 2500 F.C. at plant height with an 18 hour day length. Temperatures were kept at 72^{o} during light and 60^{o} during dark periods. Plants were watered daily and given nutrient solution once a week. After heading, the glume color was allowed to develop fully before heads were harvested and classified.

Whole spikes were collected for cytogenetic analysis while the plant was in the early boot stage. The spikes were collected between three and three and one-half hours after the lights came on, when the pollen mother cells were in the proper stage of division.

The spikes were stored at 4^{o}C. in Newcomer's solution (Newcomer 1953).

Cytogenetic analyses were made from temporary acetocarmine smears (Smith 1948) of pollen mother cells from plants of the parental and F_1 generation. The cells were analyzed for the number of univalents, open bivalents, closed bivalents, trivalents, quadrivalents and multivalents larger than quadrivalents. Anaphases were scored where possible as to the split (even or uneven), the number of laggards, and the number of bridges and fragments present. Photomicrographs were made from the temporary preparations.

The parents were not homogeneous for number of open pairs according to Bartlett's test for homogenity (Snedecor 1956), so the parents and hybrids were compared individually by T-test comparisons. All lines used in the study were disomic (2n=42).

Fertility was measured by counting the number of seed set per head in primary and secondary florets excluding the top and bottom spikelet on each head. The data was then converted to percent.

Rust tests were made and seedling rust reactions, to race 17-29, culture 58-21S-9, were determined. The rust culture (Elliott 1959) was obtained from D. M. Stewart of Minnesota and increased by Dr. A. Ellingboe of Michigan State University. Innoculations were made utilizing the method described by Rowell and Olien (1957).

The lines could be grouped into six fairly distinct classes. These classes were fleck to x^- ($F\text{-}x^-$), $1\text{-}3^x$, $1\text{-}3^s$, $2\text{-}3^{cn}$, 3 and 4. The fleck to x^- class included lines with only flecks, to those with a few small pustules surrounded by definite chlorotic rings. These plants were considered resistant. The lines which had pustule types ranging from 1 to 3 were designated $1\text{-}3^s$. The $1\text{-}3^s$ class was considered heterozygous. The $2\text{-}3^{cn}$ class had fairly consistent 2-3 size pustules with accompanying chlorotic areas surrounding the pustules and some necrosis present. Classes 3 and 4 both had large pustules with class 4 pustules being a little larger than class 3, while class 3 plants had diffuse chlorosis in the infected area and the class 4 showed chlorosis and necrosis. Class 3 and 4 were both considered susceptible.

RESULTS

CYTOLOGICAL DATA

In the course of this study, 3,284 microsporocytes were analyzed but only 1,411 are presented. Many of the parents used in crosses were heterozygous for glume color which was not known until after the cells were analyzed. All data presented is from cells in which the complete chromosome complement was countable.

There was a wide range of open pairs in the parents and hybrids. However, the mean number of open pairs in the hybrids was generally higher than in the parents. The number of cells analyzed, the means, standard deviations of the means and the ranges of open pairs are presented in Table 1.

Figure 1 presents a graphic representation of the ranges of open pairs plotted against the numbers of each class converted to percent. In this figure note that the mean and distribution of open pairs in the hybrids are not midway between but usually higher than either parent.

The mean number of open pairs in the parents were compared by means of a "T" test as were the individual parents with the hybrids to determine whether or not there was a relationship between the glume color of the parents and the number of open pairs. Table 2 shows the results of these comparisons. The diallel table is arranged so that the three red parents are grouped together, as are the white parents.

With the exception of the Hard Federation combinations, the parents are not significantly different with respect to number of open pairs, although there is variation between the parents.

Table 1. Diallel table of F_1 data giving the number of cells analyzed (N), mean number of open pairs ($\bar{x}$), standard deviations of the mean ($S\bar{x}$) and the range of open pairs (R) for all possible combinations of the six parents. TSR, 591R, and HF are red glumed and TSW, 591W and Rus are white glumed.

	TSR	591R	HF	TSW	591W	Rus
TSR	N=30 $\bar{x}$=2.7 $S\bar{x}$= .32 R=0-5	N=47 $\bar{x}$=5.74 $S\bar{x}$= .36 R=0-13		N=52 $\bar{x}$=2.98 $S\bar{x}$= .28 R=0-7	N=44 $\bar{x}$=6.34 $S\bar{x}$= .41 R=0-15	N=167 $\bar{x}$=3.58 $S\bar{x}$= .149 R=0-9
591R		N=24 $\bar{x}$=2.5 $S\bar{x}$= .346 R=0-6	N=8 $\bar{x}$=5.13 $S\bar{x}$= .55 R=3-7	N=94 $\bar{x}$=4.6 $S\bar{x}$= .26 R=0-10	N=102 $\bar{x}$=5.23 $S\bar{x}$= .243 R=1-11	N=124 $\bar{x}$=4.8 $S\bar{x}$= .203 R=0-10
HF			N=28 $\bar{x}$= .64 $S\bar{x}$=2.09 R=0-3	N=13 $\bar{x}$=5.39 $S\bar{x}$=1.03 R=0-13	N=67 $\bar{x}$=3.56 $S\bar{x}$= .216 R=0-8	N=90 $\bar{x}$=3.72 $S\bar{x}$= .223 R=1-10
TSW				N=140 $\bar{x}$=2.80 $S\bar{x}$= .26 R=0-14	N=35 $\bar{x}$=2.97 $S\bar{x}$= .37 R=0-9	N=42 $\bar{x}$=3.52 $S\bar{x}$= .29 R=0-9
591W					N=36 $\bar{x}$=3.42 $S\bar{x}$= .34 R=0-7	N=52 $\bar{x}$=5.75 $S\bar{x}$= .279 R=2-10
Rus						N=116 $\bar{x}$=3.11 $S\bar{x}$= .179 R=0-7

The data for all chromosome associations greater than bivalents is combined and expressed as the mean number of chromosomes per cell involved in such associations. This statistic, as well as the standard deviation of the mean, the range and the number of cells analyzed for each parent and hybrid, is in Table 3. The means of associations greater than bivalents are higher in the hybrids than in the parents

with the exception of the white Translocation Stock parent. This was the only parent with multivalent associations.

The "T" test comparisons between parents, together with the individual parent-hybrid combinations, show no association between glume color and number of translocations as measured by the number of chromosomes involved in association greater than bivalents. The "T" values for the comparisons are presented in Table 4. The hybrids involving either Russell or 591R are significantly different from the parents.

The data on translocations is summarized in Table 5, as determined by multivalent association, for the parents and hybrids studied. The white Translocation Stock was found to be structurally heterozygous. At least one translocation was involved in each hybrid of the diallel cross combinations. Russell, in all combinations, gave a high number of translocations, while 591R combinations, with the exception of the TSR cross, consistently have a high percentage of cells containing at least one translocation. The highest number of translocations obtained in a cross was five, between 591R and 591W. For the specific multivalent associations seen, the reader is referred to the Appendix.

There was considerable variability in the range of univalents present in the parents and hybrids. As shown in Table 6, which presents univalent data, the white Translocation Stock parent had a range of 0-8 univalents and the 591R-Rus hybrid had a range of 0-20* univalents.

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* The high number of univalents in the 591R x Rus hybrid was seen in only one cell but this one had a complete complement so was included in the analysis. If this cell were not included in the data, the range for the hybrid would have been 0-4 and the mean .952 univalents per cell. Thus, the range for this hybrid would be similar to the other hybrids involving Russell except for the one cell which, in division would undoubtedly not produce viable gametes.

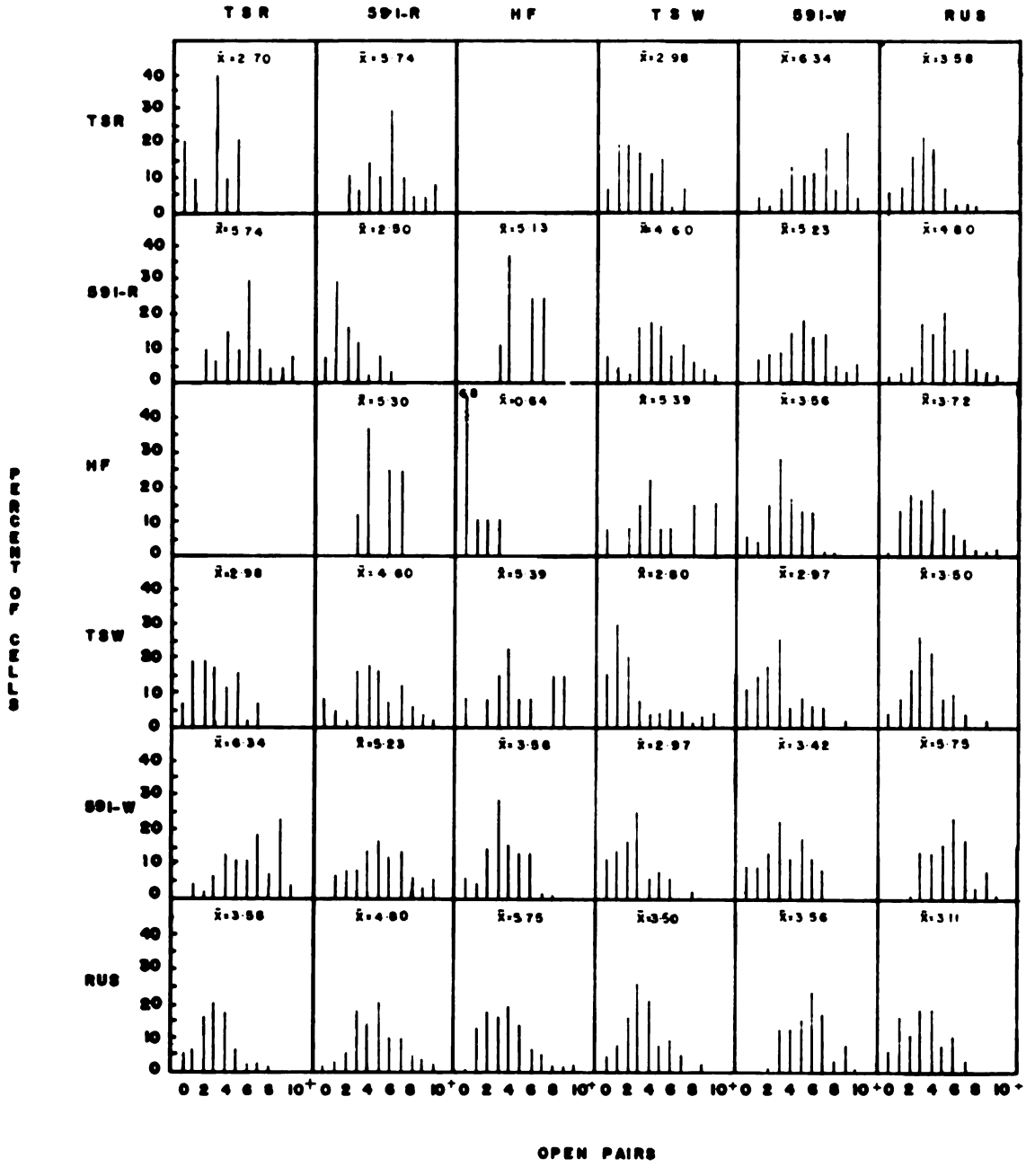


Figure 1. Graphic representation of frequency distribution of range of open pairs in parents and F_1 of diallel crosses.

Table 2. Diallel table of F_1 data giving "T" test values between parents, together with values between individual parents and the hybrids, for open pairs. TSR, 591R and HF are red glumed and TSW, 591W and Rus are white glumed.

	TSR	591R	HF	TSW	591W	Rus
TSR		TSR-591R= .42 TSR- H=5.84** 591R- H=5.70**		TSR -TSW= .173 TSR - H= .644 TSW - H= .395	TSR -591W=1.52 TSR - H=6.44** 591W- H=5.29**	TSR -Rus=1.06 TSR - H=2.33* Rus - H=1.92
591R			591R-HF=4.82** 591R-H =3.85** HF-H=9.16**	591R-TSW= .47 591R- H=3.89** TSW - H=4.74**	591R-591W=1.83 591R- H=5.19** 591W- H=3.98**	591R-Rus=1.42 591R- H=4.72** Rus - H=6.22**
HF				HF -TSW=3.68** HF - H=6.27** TSW - H=7.69**	HF -591W=6.56** HF - H=8.16** 591W- H= .36	HF -Rus=6.57** HF - H=7.41** Rus - H=7.66**
TSW					TSW -591W=1.15 TSW - H=2.39* 591W- H= .31	TSW -Rus= .95 TSW - H=1.45 Rus - H=1.20
591W						591W-Rus= .83 591W- H=5.31** Rus - H=8.13**
Rus						

Table 3. Diallel table of F_1 data showing number of cells analyzed (N), mean number of chromosomes per cell involved in associations greater than bivalents ($\bar{x}$), standard deviation of the mean ($S\bar{x}$) and range of chromosomes involved in associations greater than bivalent (R) for six parents and their crosses. Parents are grouped according to glume color.

	TSR	591R	HF	TSW	591W	Rus
TSR	N=30 $\bar{x}$=0 $S\bar{x}$=0 R=0	N=47 $\bar{x}$=.085 $S\bar{x}$=.085 R=0-4		N=52 $\bar{x}$= .385 $S\bar{x}$= .165 R=0-4	N=44 $\bar{x}$= .159 $S\bar{x}$= .112 R=0-4	N=167 $\bar{x}$= .527 $S\bar{x}$= .119 R=0-10
591R		N=24 $\bar{x}$=0 $S\bar{x}$=0 R=0	N=8 $\bar{x}$=1.75 $S\bar{x}$= .88 R=0-6	N=94 $\bar{x}$=1.38 $S\bar{x}$= .265 R=0-10	N=102 $\bar{x}$=1.80 $S\bar{x}$= .303 R=0-15	N=124 $\bar{x}$=1.21 $S\bar{x}$= .171 R=0-8
HF			N=28 $\bar{x}$=0 $S\bar{x}$=0 R=0	N=13 $\bar{x}$=1.23 $S\bar{x}$= .533 R=0-4	N=67 $\bar{x}$= .299 $S\bar{x}$= .129 R=0-4	N=90 $\bar{x}$= .667 $S\bar{x}$= .178 R=0-10
TSW				N=140 $\bar{x}$= .507 $S\bar{x}$= .192 R=0-8	N=35 $\bar{x}$= .229 $S\bar{x}$= .159 R=0-4	N=42 $\bar{x}$=1.9 $S\bar{x}$= .385 R=0-14
591W					N=36 $\bar{x}$=0 $S\bar{x}$=0 R=0	N=52 $\bar{x}$= .519 $S\bar{x}$= .215 R=0-8
Rus						N=116 $\bar{x}$=0 $S\bar{x}$=0 R=0

Results of the "T" test comparisons between the parents, together with the comparisons of the individual parents and the hybrids for the mean number of univalents, are in Table 7. There seemed to be no association between the number of univalents and the color of the parents.

Table 4. Diallel table of F_1 data showing "T" values for comparisons between parents and between parent-hybrid combinations for mean number of chromosomes involved in associations greater than bivalents. Red glumed parents, TSR, 591R and HF are together as are white glumed parents, TSW, 591W and Rus.

	TSR	591R	HF	TSW	591W	Rus
TSR		TSR-591R=0 TSR- H=.796 591R- H=.711		TSR- TSW=1.96 TSR- H=1.77 TSW- H= .533	TSR- 591W=0 TSR- H=1.16 591W- H=1.28	TSR- Rus=0 TSR- H=1.88 Rus- H=3.69**
591R			591R-HF=0 591R- H=3.55** HF- H=3.87**	591R-TSW=1.75 591R- H=2.63** TSW- H=3.96**	591R-591W=0 591R- H=2.89** 591W- H=3.54**	591R-Rus=0 591R- H=3.12** Rus- H=6.86**
HF				HF- TSW=1.896** HF- H=3.44** TSW- H=1.71	HF- 591W=0 HF- H=1.48 591W- H=1.69	HF- Rus=0 HF- H=6.59** Rus- H=4.26**
TSW					TSW- 591W=2.15* TSW- H= .812 591W- H=1.46	TSW- Rus=3.86** TSW- H=4.59** Rus- H=8.25**
591W						591W-Rus=0 591W- H=1.99* Rus- H=3.61**
Rus						

The high number of univalents in the white Translocation Stock is reflected in the significant differences between it and other parents as seen in Table 7.

Table 5. Diallel table of F_1 data showing number of cells analyzed (N), number of cells containing at least one association greater than II (N'), percent of cells containing at least one association greater than II (%), and the number of translocations, as determined by associations greater than bivalents, for parents and F_1 hybrid combinations. Parents grouped as to origin.

	TSR	TSW	591R	591W	HF	Rus
TSR	N =30 N'=0 % =0 0 Trans.	N =52 N'=5 % =9.62 1 Trans.	N =47 N'=1 % =2.12 1 Trans.	N =44 N'=4 % =9.09 2 Trans.		N =167 N'=20 % =11.98 4 Trans.
TSW		N =140 N'=20 % =14.28 2 Trans.	N =94 N'=25 % =26.59 3 Trans.	N =35 N'=2 % = 5.71 1 Trans.	N =13 N'=4 % =30.77 1 Trans.	N =42 N'=8 % =19.05 4 Trans.
591R			N =24 N'=0 % =0 0 Trans.	N =102 N'=31 % =30.39 5 Trans.	N =8 N'=3 % =37.50 2 Trans.	N =124 N'=37 % =29.84 2 Trans.
591W				N =36 N'=0 % =0 0 Trans.	N =67 N'=5 % = 7.46 1 Trans.	N =52 N'=6 % =11.54 3 Trans.
HF					N =28 N'=0 % =0 0 Trans.	N =90 N'=13 % =14.44 3 Trans.
Rus						N =116 N'=0 % =0 0 Trans.

Table 6. Diallel table of F_1 data giving number of cells analyzed (N), mean number of univalents ($\bar{x}$), standard deviation of the mean ($S\bar{x}$), and Range (R) of univalents for all cross combinations of six parent lines. Parents grouped according to glume color.

	TSR	591R	HF	TSW	591W	Rus
TSR	N=30 $\bar{x}$=.60 $S\bar{x}$=.17 R=0-2	N=47 $\bar{x}$=2.51 $S\bar{x}$= .307 R=0-8		N=52 $\bar{x}$= .346 $S\bar{x}$= .131 R=0-4	N=44 $\bar{x}$=1.07 $S\bar{x}$= .235 R=0-6	N=167 $\bar{x}$= .641 $S\bar{x}$= .094 R=0-6
591R		N=24 $\bar{x}$= .25 $S\bar{x}$= .136 R=0-6	N=8 $\bar{x}$=1.5 $S\bar{x}$= .98 R=0-8	N=94 $\bar{x}$=1.15 $S\bar{x}$= .182 R=0-10	N=102 $\bar{x}$=1.57 $S\bar{x}$= .178 R=0-6	N=124 $\bar{x}$=1.11 $S\bar{x}$= .192 R=0-20
HF			N=28 $\bar{x}$= .071 $S\bar{x}$= .071 R=0-2	N=13 $\bar{x}$=1.54 $S\bar{x}$= .46 R=0-4	N=67 $\bar{x}$= .537 $S\bar{x}$= .138 R=0-4	N=90 $\bar{x}$= .422 $S\bar{x}$= .096 R=0-4
TSW				N=140 $\bar{x}$= .88 $S\bar{x}$= 145 R=0-8	N=35 $\bar{x}$=0 $S\bar{x}$=0 R=0	N=42 $\bar{x}$=1.0 $S\bar{x}$= .229 R=0-6
591W					N=36 $\bar{x}$= .055 $S\bar{x}$= .055 R=0-2	N=52 $\bar{x}$=1.1 $S\bar{x}$=2.41 R=0-9
Rus						N=116 $\bar{x}$= .345 $S\bar{x}$= .078 R=0-4

Table 7. Diallel table of F_1 data giving "T" test comparisons between parents together with the individual comparisons of the individual parent with the hybrid (H) for the mean number of univalents.

	TSR	591R	HF	TSW	591W	Rus
TSR		TSR-591R=1.55 TSR- H=4.66** 591R- H=5.09**		TSR- TSW= .87 TSR- H=1.18 TSW- H=2.09*	TSR- 591W=3.21** TSR- H=1.48 591W- H=3.76**	TSR- Rus=1.44 TSR- H= .176 Rus= H=2.73*
591R			591R-HF=1.21 591R- H=2.09* HF- H=2.73**	591R-TSW=2.81** 591R- H= .99 TSW- H=2.54*	591R-591W=1.46 591R- H=3.54** 591W- H=4.91**	591R-Rus= .52 591R- H=1.95 Rus- H=3.61**
HF				HF- TSW=2.48* HF- H=4.93** TSW- H=1.33	HF- 591W= .16 HF- H=2.13* 591W- H=2.45*	HF- Rus=1.67 HF- H=1.98 Rus- H= .63
TSW					TSW- 591W=2.81** TSW- H=2.54** 591W- H= .99	TSW- Rus=3.07** TSW- H= .69 Rus- H=3.99**
591W						591W-Rus=1.96 591W- H=3.16** Rus- H=3.79**
Rus						

CORRELATION OF FERTILITY AND CYTOLOGICAL DATA

Ovule fertility as measured by seed set was studied in the F_1 and F_2 generations. A cytological analysis of F_1 pollen mother cells was made and the number of open pairs obtained was then correlated with F_1 and F_2 fertility data to determine the effect of the open pairs on fertility.

Data for the mean number of open pairs, the mean F_1 fertility and the standard error of the mean for fertility for each of the six parents and their hybrids are presented in Table 8.

The same information as in Table 8, but for the F_2 is shown in Table 9. There was a relatively high level of fertility in both the F_1 and F_2 but with a little more variability in the F_2.

The correlation coefficients obtained between mean fertility and mean of open pairs for the F_1 and F_2 of all possible combinations of crosses between the six parents is quite different as can be seen in Table 10. The negative correlations indicate that as the number of open pairs increased, the fertility is decreased.

Table 8. Diallel table giving mean number of open pairs ($\bar{x}$), mean F_1 fertility (F) and standard error ($S\bar{x}$) of fertility mean for six parents and all possible cross combinations between them.

	TSR	TSW	591R	591W	HF	Rus
TSR	$\bar{x}$= 2.70 F=84.50 $S\bar{x}$= 1.26	$\bar{x}$= 2.98 F=82.75 $S\bar{x}$= 8.23	$\bar{x}$= 5.74 F=85.31 $S\bar{x}$= 4.33	$\bar{x}$= 6.34 F=85.6 $S\bar{x}$= 5.44		$\bar{x}$= 3.58 F=88.11 $S\bar{x}$= 2.56
TSW		$\bar{x}$= 2.80 F=82.24 $S\bar{x}$= 4.70	$\bar{x}$= 4.60 F=87.88 $S\bar{x}$= 3.23	$\bar{x}$= 2.97 F=85.09 $S\bar{x}$= 3.93	$\bar{x}$= 5.39 F=48.34 $S\bar{x}$= 6.79	$\bar{x}$= 3.52 F=88.63 $S\bar{x}$= 3.47
591R			$\bar{x}$= 2.50 F=87.01 $S\bar{x}$= 3.23	$\bar{x}$= 5.25 F=87.26 $S\bar{x}$= 3.57	$\bar{x}$= 5.13 F=30.98 $S\bar{x}$= 7.14	$\bar{x}$= 4.80 F=86.88 $S\bar{x}$= 6.78
591W				$\bar{x}$= 3.42 F=78.21 $S\bar{x}$= 1.05	$\bar{x}$= 3.56 F=88.90 $S\bar{x}$= 0	$\bar{x}$= 5.75 F=77.28 $S\bar{x}$= 6.41
HF					$\bar{x}$= .64 F=90.60 $S\bar{x}$= 3.10	$\bar{x}$= 3.72 F=92.30 $S\bar{x}$= 2.79
Rus						$\bar{x}$= 3.11 F=90.46 $S\bar{x}$= 2.07

Table 9. Diallel table giving mean numbers of open pairs ($\bar{x}$), mean F_2 fertility (F), and standard error ($S\bar{x}$) of fertility mean for six parents and all their possible cross combinations.

	TSR	TSW	591R	591W	HF	Rus
TSR	$\bar{x}$= 2.70 F=88.97 $S\bar{x}$= 1.49	$\bar{x}$= 2.98 F=82.75 $S\bar{x}$= 8.23	$\bar{x}$= 5.74 F=73.98 $S\bar{x}$= 3.09	$\bar{x}$= 6.34 F=64.36 $S\bar{x}$= 7.06		$\bar{x}$= 3.58 F=90.34 $S\bar{x}$= 1.24
TSW		$\bar{x}$= 2.80 F=88.27 $S\bar{x}$= 1.51	$\bar{x}$= 4.60 F=73.86 $S\bar{x}$= 4.27	$\bar{x}$= 2.97 F=85.11 $S\bar{x}$= 3.92	$\bar{x}$= 5.39 F=68.56 $S\bar{x}$= 6.03	$\bar{x}$= 3.52 F=92.69 $S\bar{x}$= 1.14
591R			$\bar{x}$= 2.5 F=87.01 $S\bar{x}$= 3.20	$\bar{x}$= 5.23 F=74.74 $S\bar{x}$= 3.49	$\bar{x}$= 5.13 F=75.60 $S\bar{x}$= 7.96	$\bar{x}$= 4.80 F=80.72 $S\bar{x}$= 4.05
591W				$\bar{x}$= 3.42 F=78.21 $S\bar{x}$= 1.05	$\bar{x}$= 3.56 F=71.16 $S\bar{x}$= 7.49	$\bar{x}$= 5.75 F=77.84 $S\bar{x}$= 3.13
HF					$\bar{x}$= .64 F=90.6 $S\bar{x}$= 3.10	$\bar{x}$= 3.72 F=91.03 $S\bar{x}$= 1.82
Rus						$\bar{x}$= 3.11 F=90.46 $S\bar{x}$= 2.07

Table 10. Correlation coefficients between open pairs and F_1 and F_2 fertility.

Parental Combinations	F_1 "r" Value	F_2 "r" Value
TSR	.2531	-.909*
TSW	-.6891	-.808*
591R	-.2145	-.881**
591W	-.0939	-.637
HF	-.7290	-.697
Rus	-.8826**	-.949**

GLUME COLOR STUDY

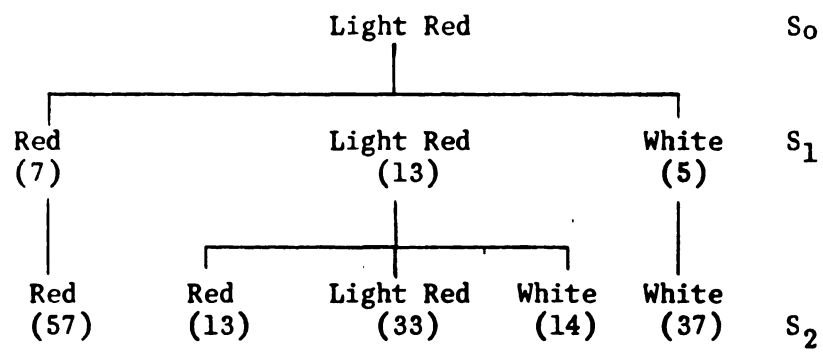
The genetics of glume color was studied in the F_1 and F_2 generations of a diallel involving six parents. It was also studied through three selfed generations of the red and white glumed lines of the Translocation Stock.

Figure 2 shows the three classes of glume color obtained as segregates from a light red plant. These heads were taken from the F_2 segregating population of a single F_1 light red plant.

Figure 2. The three classes of glume color obtained in the growth chamber under optimum conditions for glume color development. Left to Right: White, Light Red, Red.

The results from three selfed generations of the Translocation Stock indicate the inheritance pattern of glume color. Figure 3 shows the inheritance pattern and pooled data on the color segregates obtained from three lines tested for three generations.

Figure 3. Inheritance pattern of glume color in translocation stock and pooled numbers obtained from 3 lines.



The segregation data for the three selfed generations of the translocation stock were tested for closeness of fit to a 1:2:1 ratio by means of a chi square test. Table 11 shows the fit obtained by a chi square test in the S_1 generation only. Deviations from a 1:2:1 ratio as large as observed would be noted 84.7 percent of the time by chance alone, a good fit.

Table 11. Chi square for glume color inheritance for a 1:2:1 expectation for S_1 generation.

Color	Obs.	Exp.	Dev.	$\frac{Dev.^2}{Exp.}$
Red	7	6.25	+ .75	.09
Light Red	13	12.5	+ .5	.02
White	5	6.25	-1.25	.25
Totals	25		x^2 = .360 P = .847	

Table 12 presents the chi square test for the S_1 and S_2 pooled data. Deviations from a 1:2:1 ratio as large as observed would be noted in 50.7 percent of the time due to chance alone.

Table 12. Chi square for glume color inheritance for a 1:2:1 expectation. S_1 and S_2 data is pooled.

Color	Obs.	Exp.	Dev.	$\frac{Dev^2}{Exp.}$
Red	20	21.25	-1.25	.735
Light Red	46	42.50	+3.50	.288
White	19	21.25	-2.25	.238
Totals	85		$x^2 = 1.261$ $P = .507$	

Table 13 shows the F_1 glume colors and the F_2 segregation data obtained from the diallel cross. The F_1 hybrids between red glumed and white glumed lines had light red glume color and these segregated for red, light red and white in the F_2 generation. No segregation was observed in crosses involving red glumed parents or white glumed parents.

There is no F_2 data for the TSR x HF cross since the seed for that generation was taken from a plant involving a heterozygous translocation which was not revealed until progeny tests of the parent lines were grown concurrently with the F_2 generation.

Table 13. Parental, F_1 and F_2 results of diallel cross involving six parents to test glume color inheritance. R=Red, LR=Light Red, W=White. Parents grouped according to glume color.

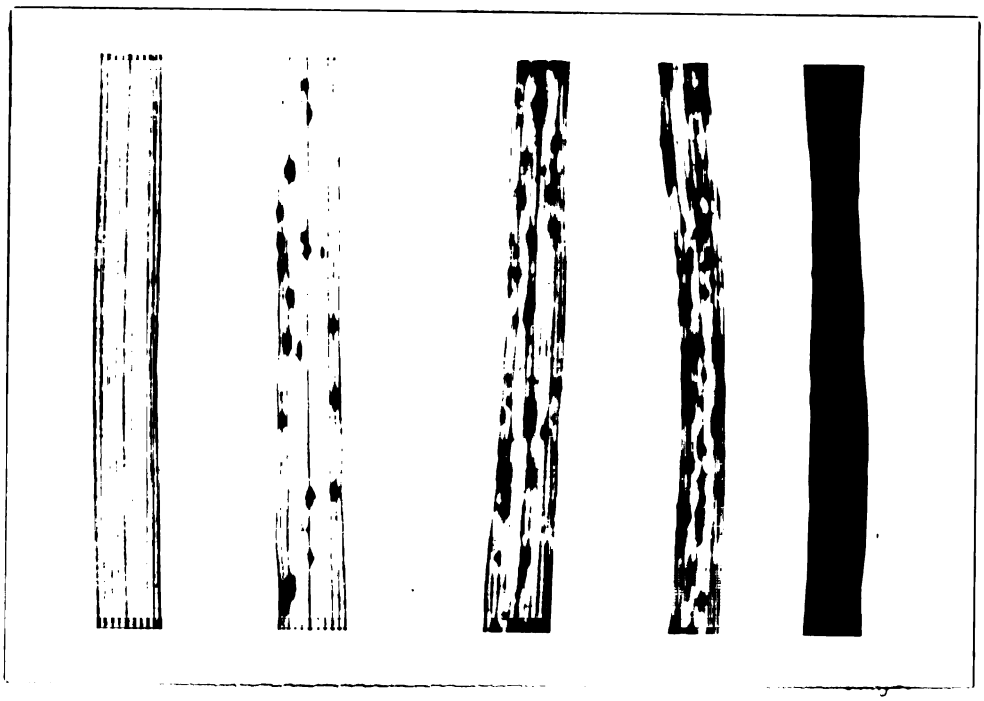
		TSR			591R			HF			TSW			591W			Rus		
		R.	L.R.	W.	R.	L.R.	W.	R.	L.R.	W.	R.	L.R.	W.	R.	L.R.	W.	R.	L.R.	W.
TSR	F_1	x[1]	0	0	x	0	0	x	0	0	0	x	0	0	x	0	0	x	0
	F_2	57	0	0	35	0	0		----		1	8	2	10	3	4	14	8	5
591R	F_1				x	0	0	x	0	0	0	x	0	0	x	0	0	x	0
	F_2				28	0	0	8	0	0	12	13	6	5	8	6	14	6	6
HF	F_1							x	0	0	0	x	0	0	x	0	0	x	0
	F_2							29	0	0	9	12	3	0	6	3	4	9	4
TSW	F_1										0	0	x	0	0	x	0	0	x
	F_2										0	0	37	0	0	9	0	0	31
591W	F_1													0	0	x	0	0	x
	F_2													0	0	15	0	0	17
Rus	F_1																0	0	x
	F_2																0	0	28

1. x = all plants were color indicated

STEM RUST INVESTIGATIONS

There was a wide range in the rust reactions of the Translocation Stock from resistant to susceptible. The reactions in Figure 4 are typical of the classes observed.

Figure 4. Infection types used in classifying the reaction of lines and crosses tested to Race 17-29, culture 58-21S-9. Left to Right: F, F-x^{-}, 1-3^{x}, 3, 4.



Rust reaction and glume color were independently inherited in these materials. This is illustrated in Table 14. The rust reactions and glume colors were verified by progeny tests.

The rust reaction of Kenya Farmer to the race and culture used was consistently different from the Translocation Stock reactions and easily distinguishable. All samples of Kenya Farmer and only Kenya Farmer gave the 2-3^{cn} type of reaction in both tests. The Translocation

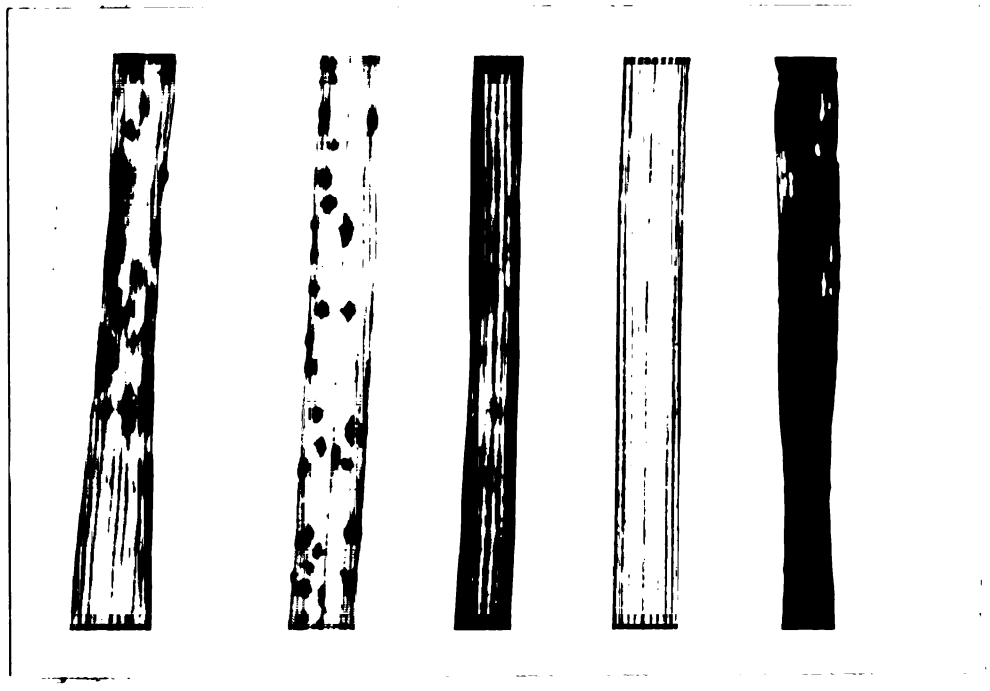
Stock lines varied in their reaction from resistant to susceptible and in amounts of chlorosis but were easily separated from Kenya Farmer lines.

Table 14. Glume colors and stem rust reactions to three different plant lines. RR=Red, Rr=Light Red, rr=White.

Plant Lines	Glume Color	Rust Reaction
T.S. 315	RR	F (Resistant)
T.S. 315	Rr	F (Resistant)
T.S. 315	rr	F (Resistant)
T.S. 36	Rr	$1\text{-}3^{x}$ (Mesothetic)
T.S. 36	RR	$1\text{-}3^{x}$ (Mesothetic)
T.S. 11	RR	4 (Susceptible)
T.S. 11	Rr	4 (Susceptible)
T.S. 11	rr	4 (Susceptible)

Figure 5 shows the reaction type obtained from Kenya Farmer ($2\text{-}3^{cn}$) and the range of reaction types in the Translocation Stock (F to 4). Also included in the picture are the reactions of Idaed, the susceptible parent of the Translocation Stock (3-4), and the octaploid (n=56) Agropyron elongatum-Triticum derivative parent ($F\text{-}x^{-}$) from which the Translocation Stock obtained its resistance.

Figure 5. Differences observed in reaction type between Kenya Farmer and the Translocation Stock, together with the stem rust reactions of the parents involved in the Translocation Stock. Left to Right: Kenya Farmer, Idaed, octaploid parent, two Translocation Stock lines.



The rust reactions of some crosses were studied to get information on the inheritance of the rust reaction of the Translocation Stock. The parental and F_2 rust reaction of a cross between Kenya Farmer and a Translocation Stock line is presented in Table 15. The F_2 showed segregation for rust reaction indicating heterozygosity.

As shown in Figure 6, 591R and 591W gave different types of reactions. The pustule size is slightly larger in 591W and in addition there is considerable chlorosis accompanying the 591W infection whereas there is no chlorosis accompanying the 591R infection.

Table 15. Stem rust reactions of the parents involved and a cross between the Translocation Stock and Kenya Farmer.

Lines	Generation	Reaction
TS 315	P	F (Resistant)
Kenya Farmer	P	$2\text{-}3^{cn}$
TS 315 x Kenya Farmer	F_2	$1\text{-}3^{s}$

Figure 6. Rust reactions of 591R and 591W. 591R is on the left.

In a cross between a Translocation Stock line and 591W, Table 16, there was no segregation observed in the F_1 or the F_2 generations.

Table 16. Stem rust reactions of the parents involved and two generations of a cross between the Translocation Stock and 591W.

Lines	Generation	Reaction
T.S. 1	P	3-4
591W-16	P	3-4
T.S. 1 x 591W-16	F_1	3-4
	F_2	3-4

Table 17 gives the rust reactions of a cross between a Translocation Stock line and 591R. The reaction in this cross is not the same as the 591W x Translocation Stock cross shown in Table 16.

Table 17. Stem rust reactions of parents involved and a cross between the Translocation Stock and 591R.

Lines	Generation	Reaction
T.S. 16	P	3-4
591R-68	P	3-4
T.S. 16 x 591R-68	F_2	$1\text{-}3^s$
	F_3	$F\text{-}\bar{x}$

DISCUSSION

CYTOLOGICAL STUDIES

Open Pairs

Cytological analysis of meiosis in the F_1 hybrids of the diallel revealed a high level of structural heterozygosity, which is maximized in this generation. An average of two or three open pairs is usually considered normal in wheat due to the presence of two or three chromosomes with non-median centromeres which, at metaphase I form open rather than closed pairs.

The open pairs may result from several causes. Small translocations of a reciprocal as well as a non-reciprocal nature, including intercalary insertions, may interfere with pairing and result in open pairs rather than the multivalent associations commonly observed in large reciprocal translocations. Small inversions may also cause open pairs. Other factors governing the formation of open pairs are location, number and rate of terminalization of chiasma.

In this study, the open pairs observed were considered to be primarily a result of translocations, as indicated by the reduction in number of open pairs in cells which contained multivalent associations. However, the number of translocations present could not be determined from open pair data alone. The high number of open pairs in the hybrids primarily serves as a good indication of the presence of translocations.

As shown by the means in Table 1, the parents had fewer open pairs than the hybrids. The means of the parents were from .64 to 3.42

while the means of the hybrids ranged from 2.97 to 6.34. The variation observed between parental means must be considered in drawing conclusions from the open pair data and may be reflected to a certain extent in the range of hybrid means.

The two tester stocks for the studies of glume color (Hard Federation and Russell) were chosen because of their glume color, red and white, respectively. Their karyotypes, however, were not similar. They serve as good examples of the present evolution or change in karyotypes as a result of breeding. Plant breeders, in introducing disease and insect resistance through wide crosses and irradiation programs, are continually changing the karyotype of present day wheats. An example of this change is the level of open pairs in Hard Federation and Russell. Their difference in karyotype is attributed to their pedigrees and the effect of introducing foreign chromatin into a species is seen in chromosome pairing relationships.

The histograms in Figure 1 present the range and frequency distributions of open pairs for each parent and hybrid and should facilitate comparisons between them. A comparison of parents and their hybrids shows an increased frequency of higher numbers of open pairs. This structural heterozygosity in the hybrids is due to the presence of translocations or the lack of structural homology between varieties.

There was a wide range of open pairs in the hybrids and the white Translocation Stock parent. This parent had a range of 0-14 open pairs while the widest range of the hybrids was 0-15 open pairs in the TSR x 591W hybrid. The frequency distributions in Figure 1, however, clearly illustrate the difference between the TSR x 591 hybrid and

the TSW parent. They indicate that only a few cells of the TSW parent had a high number of open pairs. While the ranges of the other parents were not as wide as the white Translocation Stock, their open pair frequencies, like most of the TSW parent, were generally higher for low numbers of open pairs than were the hybrids.

Bartlett's test showed that the parents were not homogeneous for the number of open pairs. As a result, the parents were compared in two's by the "T" test for differences in open pairs as were the hybrids. The comparisons presented in Table 2 show no association between glume color and number of open pairs. There is, however, some evidence of an association between open pairing and parental origin. Hard Federation is significantly different from all other lines used as parents with respect to the number of open pairs. Most Hard Federation cells examined had no open pairs but a few had from 1-3. This is in contrast to the other parents which had induced mutations, or chromatin other than vulgare in their pedigrees and a wider range of open pairs.

Multivalents

While open pairs in wheat are fairly good indicators of translocations, multivalent associations must be found in order to confirm their presence. From the size of the association seen, a minimal estimate of the number of translocations can be obtained.

The level of multivalent associations found in this study was relatively low, considering the high number of open pairs. However, at least one multivalent association was found in each hybrid. Associations of six, eight, ten and twelve chromosomes were observed

and examples of these associations and the configurations seen in the individual crosses are in the Appendix.

According to "T" test values for the multivalent associations, there is more of a relationship between parental origin and multivalent associations than glume color and multivalent associations. The significant differences between Russell and its hybrids and likewise 591R and its hybrids, indicate the effect of breeding and induced mutations on the karyotype. The lack of relationship between karyotype and glume color may result from the condition that the factor(s) governing glume color are not affected by the translocations or the translocation effect is being masked as a result of the buffering in wheat.

The white Translocation Stock used as a parent was found to be structurally heterozygous and to contain at least two translocations (see Table 5). As a result, any comparisons involving it may be somewhat biased.

The relatively consistent percentage of cells which contain translocations in the 591R hybrids is taken as an indication that there was at least one fairly large translocation which occurred in the origin of the 591R line. As a result, multivalent associations form in combinations with other varieties to satisfy pairing relationships.

Univalent Behavior

There were univalents present in all parents and hybrids with the exception of the TSW x 591W hybrid. As was the case with open pairs

and multivalent associations, the heterozygosity of the TSW parent is again observed in univalent data.

In the "T" test comparisons, between parents and hybrids for number of univalents, the high number in the TSW parent is indicated by the significant difference between it and the other parents.

No detectable phenotypic effect was associated with the presence of univalents. As seen in Figure 9F in the Appendix, as many as four univalents were observed to be lagging in division on the plate. The half chromosome moved randomly to the poles after division in anaphase I.

Inversions were seen in some cells as indicated by the example in Figure 9G in the Appendix. This photograph shows the presence of two inversions in a cell as indicated by two bridges and fragments (McClintock 1938).

Implications of Variations in Karyotypes

There are several practical implications in breeding research which may be drawn from the observed differences in karyotypes between varieties.

The structural differences between varieties and structural rearrangements induced by mutational processes have the effect of suppression of recombination through lack of pairing. The usual concept of irradiation to produce mutation and variability through recombination, when carried a step further to the structural level, may actually have the reverse effect because the structural rearrangements will result in decreased recombination and variability due to lack of pairing.

The establishment of a "wild type" in wheat, as in Drosophila, has been proposed by some wheat geneticists. In view of the karyotypic variability between varieties, as shown in this study, the choice of a "wild type" would not be meaningful. Wheat is a hexaploid and while it behaves as a diploid in some respects, in others it does not. It has a residual heterozygosity which is not observed in the phenotype as a result of its origin through duplication and combination of genomes. Structurally, however, this variability is easily observed by cytological analysis.

Another consideration involving karyotypic variability is the use of irradiated material in breeding programs. The reduction in fertility associated with an increase in the number of open pairs stresses the importance of backcrossing the irradiated material to a standard variety for several generations before use in hybrid programs. This should be done to impose the karyotype of the recurrent parent on the non-recurrent parent so that better recombination of genetic material can be obtained in crosses.

CYTOGENETIC RELATIONSHIPS

Open Pair Fertility Correlation

The F_1 fertility of two of the hybrids was low. However, the F_2 fertility of these two hybrids was more in the range of the other hybrids. The reduction in fertility of the Hard Federation combinations with the white Translocation Stock and the 591 lines is possibly related to an observed dwarfing effect of the Hard Federation combinations.

There was no correlation in the F_1 between the number of open pairs and the ovule fertility as measured by seed set. There was, however, a high negative correlation between open pairs and F_2 fertility. Such a correlation in the F_2 was not expected. Genic control of fertility with segregation in the F_2 may account for the lack of correlation in the F_1.

The highest and most significant correlations between fertility and mean number of open pairs were obtained in the combinations involving the red and white glumed Translocation Stocks, the 591R parent and Russell. These parents are derived from induced mutations or translocations while Russell has T. dicoccum and T. durum in its pedigree. As a result, their karyotypes have been altered and the relationship of structural homology and fertility is thus illustrated.

Rust Reaction and Structural Association

In the rust tests a difference in reaction types was observed between the seedling rust reactions of 591R and 591W. In the 591W cross only susceptible plants were obtained in the F_1 and F_2 generations whereas in the 591R cross, the F_2 was classed as $1\text{-}3^S$ and the F_3 as $F\text{-}x^-$ or resistant.

To explain the above results the presence of a complementary factor type of relationship or modifying factors is suggested. Stewart (1963) found that six Marquis substitution lines developed by backcrossing did not have the same resistance as the donor varieties. He pointed out that it is not clearly understood how a gene will react when placed in a different genetic background and that unknown modifying factors may operate when a gene is transferred out of its

genetic background. The reaction differences observed in the 591R and 591W crosses to the susceptible Translocation Stock may be a result of placing the genes in a different genetic background similar to that reported by Stewart.

However, since 591R was produced as a mutant, by peanut oil treatment of 591W, and the hybrid between 591R and 591W showed a difference of at least five translocations, the difference in reaction may be attributed to chromosomal rearrangement which took place as a result of the peanut oil treatment. This difference in reaction was quite noticeable and the association or causal mechanism should be further studied.

Origin of Light Red Chimera

Research on progeny of the light red chimera and the remainder of the plant revealed three facts about the origin of the chimera. These must be explained by any acceptable theory of its origin and are as follows: (1) The mutation causing the light red section must have occurred very early in the embryo development of the plant and involved a structural rearrangement as there were at least two translocations in the white Translocation Stock and one in the hybrid between the red and white Translocation Stocks; (2) Segregation for glume color occurred in progeny of the light red chimera and (3) Both the normal and chimeral sections had 42 chromosomes.

A few reports in the literature are pertinent to the discussion of the origin of the light red chimera.

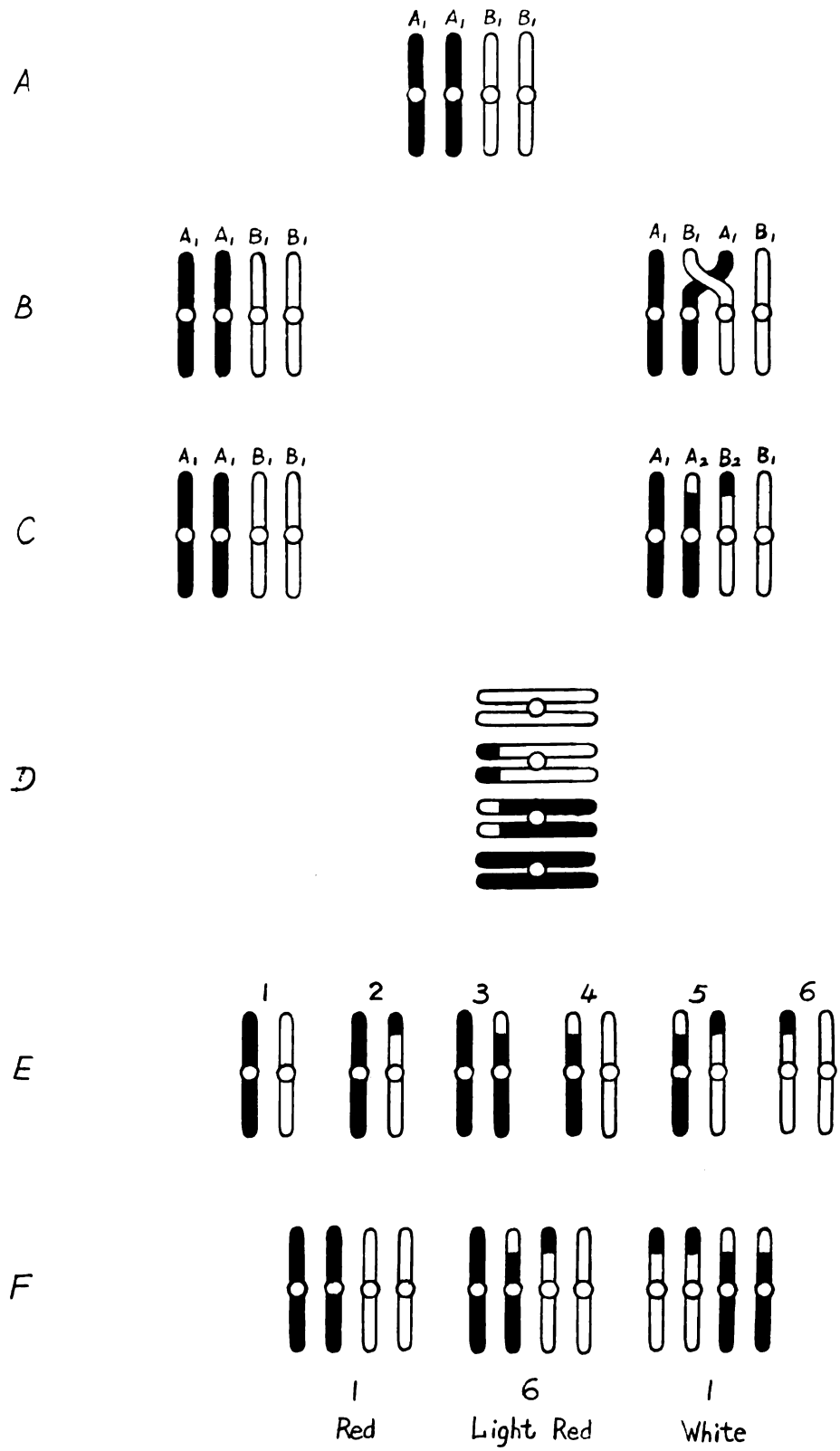
Morey (1949) studied the causes of a mutant type in Clinton oats which appeared frequently. He examined many possibilities and concluded, after a cytological study of the material, that the mutant type arose as a result of a chromosomal rearrangement probably a deletion. Huskins and Sanders (1949) studied the cause of speltoid, compactoid and sub-normal wheats and found that they result from deficiencies ranging from whole chromosomes down to minute fragments.

Love (1938) made a cytogenetic study of a white chaff off type occurring in Dawson's Golden Chaff, a red glumed wheat. He reported that red glume color was manifested in the presence of a complete chromosome complement, light red color with one chromosome carrying the locus for red color and a terminal deficiency of the locus in the other member of the pair and white glumes when both chromosomes of the pair were deficient for the critical section. Love's study provides a basis for the origin of the light red chimera found in the X_4 generation of the red Translocation Stock.

The red glume color in the original Translocation Stock may have resulted from a position effect associated with one of the original translocations shown to have taken place (Elliott, 1957). The mutational event causing the light red chimera must have arisen in the somatic tissue very early in the formation of the embryo of the plant to affect about half the plant.

This mutation may have resulted from a non-homologous somatic exchange of segments. Presumably, the segments involved in the exchange re-established the original chromosome structure existing prior to the initial irradiation in one chromosome. As a result of the exchange,

Figure 7. Origin of light red chimera. (A) Two chromosome pairs $A_1A_1B_1B_1$ in red Translocation Stock. (B) Early mitosis showing normal chromosomes in one cell ($A_1A_1B_1B_1$) and non-homologous cross over and break in another cell. (C) Products of mitosis from cell in red glumed section giving $A_1A_1B_1B_1$ red glumed and cell in light red section giving $A_1A_2B_1B_2$ light red glumed. (D) Chromosomes from cell of light red glume chimera in meiosis I. (E) Six types of gametes formed. (F) Viable combination functional as zygotes.


A
A1 A1 B1 B1
B
A1 A1 B1 B1
A1 B1 A1 B1
C
A1 A1 B1 B1
A1 A2 B2 B1
D
E
1 2 3 4 5 6
F
1
Red
6
Light Red
1
White

the pair controlling glume color was left in the heterozygous condition. This pair then, through subsequent mitotic divisions resulted in the light red half of the plant.

Cytological analysis of the white Translocation Stock showed that open pairs, as indications of translocations were much more prevalent than multivalent associations. At meiosis, therefore, segregation would be primarily from open pairs. Such segregation would produce six types of gametes in equal numbers. Upon selfing, if all gametes can combine at random, 36 types of zygotes are possible. If it is then assumed that zygotes containing duplications and/or deficiencies are not functional, eight out of the 36 possible zygotes would be functional. These would be in the ratio of 1:6:1, normal to translocation heterozygote to translocation homozygote respectively. According to Love's findings on the relationship of chromosome structure to glume color, the above zygotes would produce one red to six light red to one white glumed plants. This is similar to the ratio of 1:8:2 which was obtained from glume color data. A chi square test showed that deviations from the 1:6:1 ratio as large as observed would be expected 88.3 percent of the time by chance alone. Considering sample size, this is a very good fit.

The F_1 fertility of the TSR-TSW hybrid was 82.75 ± 8.23. The fertility, according to the hypothesis, would be about 70% if there were six types of gamets formed and all four linear megaspores were assumed to be functional. If selectivity for one of the megagametes were operating or there was a differential rate of pollen tube growth, the difference between the observed and expected fertilities could be reconciled.

The hypothesis proposed presents a good example of a reversal of a position effect. It would explain the segregation obtained from the light red chimera, the presence of the translocation in the hybrid between homozygous red and white lines and the disomic condition obtained in both the normal and chimera sections of the original plant.

GENETIC STUDIES

Glume Color

In the field locally, full expression of glume color is not obtained due to weathering and classification is usually difficult. In contrast to this, observations on the glume color development of wheats grown in the growth chamber could be grouped into three fairly distinct categories. These were designated as red, light red and white.

The environmental conditions in the growth chamber allow the full expression of glume color.

Progeny testing of the three glume color categories revealed that the red and white lines were true breeding whereas the light red class segregated into red, light red and white. Considering sample size, chi square tests indicated a good fit to a 1:2:1 ratio. Hybrids between red and white glumed varieties were light red in the F_1 and segregated in the F_2 while in crosses between red glumed lines or between white glumed lines no segregation was observed in the F_2. This indicated that red glume color was incompletely dominant over the white glume color. Since there was no segregation for color in crosses between red glumed varieties (and also white) the gene(s) controlling glume color may be at one locus in the lines studied.

Although the populations were small, it appeared that glume color was simply inherited.

The Translocation Stock materials used as parents in this study were chosen on the basis of glume color classification in the field. The segregating nature of the light colored chimera was not then known, and a misclassification in the field of some of the Translocation Stock lines used as parents resulted. Consequently, there was a deficiency of some critical crosses and small populations obtained in certain crosses.

No red segregates were obtained in the F_2 of the cross between 591W and Hard Federation. However, since segregation did occur in the F_2, the absence of red segregates is attributed to small sample size.

It has been demonstrated in this study that, under controlled conditions, wheat lines heterozygous for glume color can be separated phenotypically from homozygotes. This should prove to be a valuable tool to the wheat breeder in producing varieties which will breed true for glume color. Seed certifying groups could also clean up released varieties which have off type or color segregates present. The lines to be screened could be grown in the growth chamber for one or two generations and selections made for pure lines homozygous for red or white glume color.

RUST STUDIES

No association was observed between glume color of the Translocation Stock and rust reaction to the particular rust culture used.

The original Translocation Stock was heterozygous for its rust reaction. This is shown by the range from resistant to susceptible obtained from different plant lines.

The resistant and susceptible plant progeny gave the same reactions as their parents. The resistant segregates had a very high degree of resistance to the culture used and should have good potential as a source of stem rust resistance.

Future rust studies with the translocation should include testing of the resistant lines to different races of stem rust to determine the extent of the resistance present. Crosses should be made between resistant and susceptible lines and the progeny tested to determine the inheritance of resistance in the Translocation Stock, the number of genes involved and their action. Crosses between resistant lines and rust tests of their progeny would test for allelism.

For the above tests, on the basis of rust results obtained, T.S. 312, T.S. 33, T.S. 315, T.S. 307, T.S. 305 and T.S. 299 have been found to be resistant while T.S. 11, T.S. 1, T.S. 16, T.S. 311 and T.S. 291 have been found to be susceptible.

Two approaches to the clarification of the immediate source of resistance in Elliott's Translocation Stock were tested. If the translocation stock was a result of outcrossing to Kenya Farmer, the reaction of the two wheats should be similar to the rust culture. However, this was not the case. Seedling rust tests comparing the Translocation Stock and Kenya Farmer showed little similarity between the two varieties, as determined by their rust reaction to Race 17-29 culture 58-21S-9. This result, together with the results of the two varieties in the world rust test in which Kenya Farmer had an average coefficient of infection of 13 and the Translocation Stock 6.5, (Loegering 1962) indicate the dissimilarity of Kenya Farmer and the Translocation Stock.

Another method of clarifying the immediate source of resistance in the Translocation Stock would be to make crosses between Kenya Farmer and the Translocation Stock and observe the rust reactions of the progeny. Segregation occurred in the F_2 of such a cross, further indicating the dissimilarity of the Translocation Stock rust resistance and that of Kenya Farmer.

CONCLUSIONS

A mechanism for the origin of the light red glumed chimera was proposed based on the reversal by a non-homologous segment exchange, of a position effect which resulted from an induced translocation.

In the study of the inheritance of glume color in Elliott's Translocation Stock, the observed ratios gave a good fit to an expected 1:2:1 ratio indicating that the glume color was simply inherited. It was also demonstrated in this study that the heterozygous class (light red) could be phenotypically distinguished from the homozygotes.

Glume color and rust reaction were found to be independently inherited in Elliott's Translocation Stock but there was a difference in reaction observed between the 591R and 591W lines.

No segregation occurred in the F_2 of crosses between red glumed varieties (also white glumed) so it could be concluded that the gene(s) controlling glume color appear to be at the same locus in the lines studied.

The karyotypic analysis revealed a high level of structural heterozygosity in the hybrids analyzed, but a clear relationship could not be established between glume color and structural arrangements. The analyses, however, revealed considerable variation in open pairs between varieties developed with complex pedigrees and simple pedigrees. This variation illustrated the effect of breeding programs on the evolution of the karyotype.

Since the rust reactions of Kenya Farmer and Elliott's Translocation

Stock showed little similarity to the race tested and segregation occurred in the F_2 of a Kenya Farmer x Translocation Stock cross, it may be concluded on the basis of rust reactions that the immediate source of resistance of the Translocation Stock did not come from Kenya Farmer.

APPENDIX

Figure 8. Microsporocytes showing range of open and closed bivalents; A. Diakinesis, 20 closed II, 1 open II; B. Diakinesis 19 II, 1 IV; C. Diakinesis 21 closed II; D. MI. 5 open II, 16 closed II; E. MI. 11 open II, 10 closed II, F. MI. 4 I, 8 open II, 11 closed II. Divisions on scale = .02 mm.

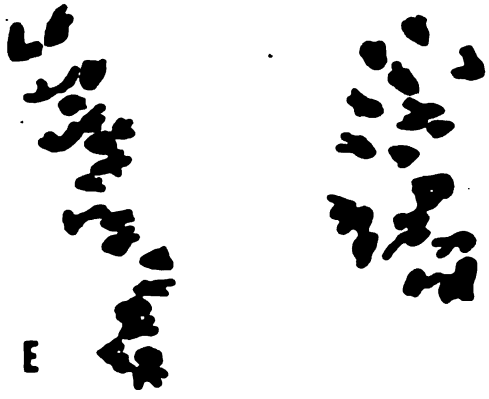

A
B
C
D
E
F

Figure 9. Microsporocytes showing range of multivalent associations observed. A. MI. 1 open II, 18 closed II, 1 IV; B. 9 open II, 10 closed II, 1 IV; C. MI. 4 open II, 15 closed II, 1 IV; D. MI. 2 I, 4 open II, 12 closed II, 2 IV; E. MI. 4 I, 4 open II, 10 closed II, 1 IV, 1 chain of 6; F. MI. 3 open II, 14 closed II, 1 chain of 8; G. Drawing of chain of 8 in Fig. 8F. Divisions on scale - .02 mm.

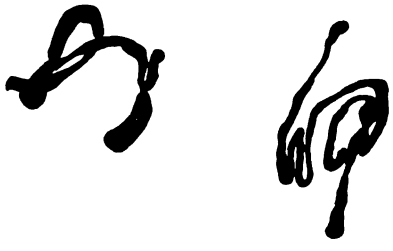

A
B
C
D
E
F
G

Figure 10. Miscrosporocytes showing multivalent associations, anaphase divisions, lagging chromosomes in division and bridges and fragments. A. MI. 16 closed II, 1 chain of 10; B. Drawing of chain of 10 in Fig. 9A; C. Drawing of chain of 12 in Fig. 9D (should be rotated 90° to left to be properly oriented); D. MI. 4 I, 2 open II, 11 closed II, 1 chain of 12; E. Normal anaphase with equal separation; F. Anaphase I with 4 univalents lagging in division; G. Anaphase I with 2 bridges, 2 fragments and a pair of lagging univalents. Divisions in scale - .02 mm.

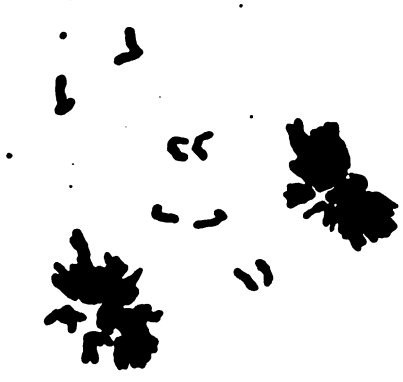
A



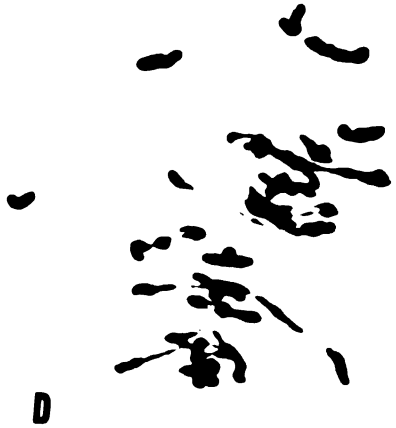
E



B C



F



D

G

CYTOLOGICAL CONFIGURATIONS OBSERVED

TSR

1. No multivalents
2. Bridge and fragment
3. Up to four lagging chromosomes
4. Equal and unequal separation

TSR x TSW

1. Associations of four
2. No anaphase cells analyzed

TSR x 591R

1. Associations of four
2. Equal and unequal separation

TSR x 591W

1. Chain of six chromosomes
2. Two quadrivalents in one cell
3. Up to two bridges alone and with fragments
4. Up to three lagging chromosomes
5. Equal and unequal separation

TSR x Rus

1. Chain of 10 chromosomes
2. Associations of four chromosomes
3. Up to three bridges mostly without fragments
4. Up to two lagging chromosomes
5. Equal and unequal separation to the poles

TSW

1. Chain of six chromosomes
2. Two associations of four chromosomes in one cell
3. Single associations of four chromosomes
4. Trivalents plus univalent
5. Up to four lagging chromosomes
6. One monosomic plant
7. Asynapsis in some cells of one plant

TSW x 591R

1. Chain of eight chromosomes
2. Chain of six chromosomes plus an association of four chromosomes
3. Chain of six chromosomes
4. Two associations of four chromosomes
5. Single associations of four chromosomes
6. Trivalents plus univalents
7. One and two bridges without fragments
8. Up to four lagging chromosomes
9. Equal and unequal separation to the poles

TSW x 591W

1. Association of four
2. No univalents found
3. No anaphase cells analyzed

TSW x HF

1. Associations of four
2. Bridge and fragment
3. Up to six lagging chromosomes

TSW x Rus

1. Chain of 10 chromosomes
2. Two open associations of four plus a chain of six chromosomes
3. Chain of six chromosomes
4. Associations of four

591R

1. No multivalents
2. No anaphases analyzed

591R x 591W

1. Chain of twelve chromosomes
2. Chain of eight chromosomes plus a quadrivalent
3. Chain of six
4. Three quadrivalents in one cell
5. Two quadrivalents
6. Single quadrivalents
7. Trivalents plus univalents
8. Bridge and fragment
9. Up to four lagging chromosomes
10. Equal and unequal separation to the poles

591R x HF

1. Chain of six
2. Single quadrivalents
3. Bridge but no fragment

591R x Rus

1. Quadrivalents
2. Single quadrivalents
3. Trivalents plus univalents
4. Two bridges and fragments
5. Up to four chromosomes lagging

591W

1. No multivalents
2. No anaphase cells analyzed

591W x HF

1. Single quadrivalents
2. Two chromosomes lagging

591W x Rus

1. Chain of eight chromosomes
2. Single quadrivalents
3. Trivalents plus univalents
4. Up to three chromosomes lagging

HF

1. No multivalents - mostly closed bivalents
2. No bridges or laggards observed

HF x Rus

1. Chain of six chromosomes plus a quadrivalent
2. Single quadrivalent
3. Trivalent plus univalent
4. Bridge but no fragment
5. Up to three chromosomes lagging

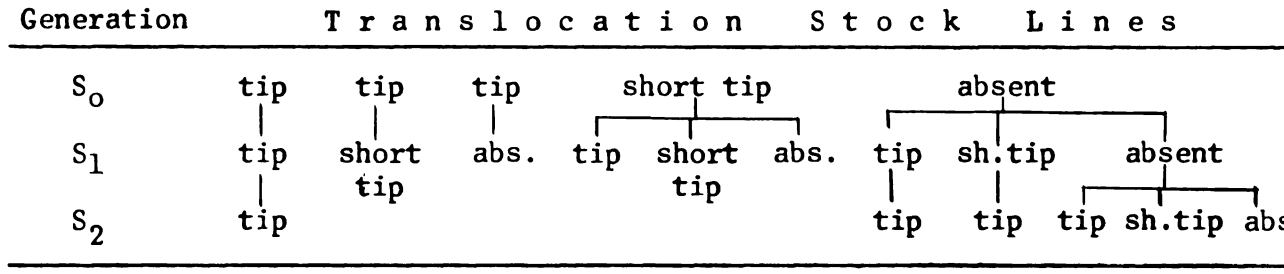
Rus

1. No multivalents
2. One tetrasomic cell

AWNING OBSERVATIONS

The type of awn present on selfed lines of the Translocation Stock was recorded for two and three generations. Figure 8 shows some of the types of awns produced from different lines of the Translocation Stock.

Figure 11. Examples of variation of awn types produced from selfed lines of the Translocation Stock.



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