

A STUDY OF THE RELATIONSHIP AND
PERFORMANCE OF PARENTAL RYE LINES,
THEIR TOP-CROSSES, AND THEIR
TRITICALE AMPHIDIPOIDS

A Thesis
Submitted to the Faculty
of
Graduate Studies
The University of Manitoba
by
Kenneth William May

In Partial Fulfillment of the
Requirements for the Degree

of

Doctor of Philosophy
Department of Plant Science
November 1976

**"A STUDY OF THE RELATIONSHIP AND
PERFORMANCE OF PARENTAL RYE LINES,
THEIR TOP-CROSSES, AND THEIR
TRITICALE AMPHIDIPLOIDS"**

by

KENNETH WILLIAM MAY

**A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of**

DOCTOR OF PHILOSOPHY

© 1977

**Permission has been granted to the LIBRARY OF THE UNIVER-
SITY OF MANITOBA to lend or sell copies of this dissertation, to
the NATIONAL LIBRARY OF CANADA to microfilm this
dissertation and to lend or sell copies of the film, and UNIVERSITY
MICROFILMS to publish an abstract of this dissertation.**

**The author reserves other publication rights, and neither the
dissertation nor extensive extracts from it may be printed or other-
wise reproduced without the author's written permission.**

ACKNOWLEDGMENTS

I wish to express my sincere appreciation to my advisor, Dr. E. N. Larter, Department of Plant Science, for his encouragement and guidance throughout the course of the investigation and for his critical review of the manuscript. Thanks are also extended to Dr. L. Evans, Dr. L. LaCroix, Dr. C. Bernier, Dr. B. Irvine, and Dr. E. Reihbergs for their valuable advice and review of the manuscript.

I wish to express my gratitude to the Department of Plant Science for the provision of facilities and to all members of the Department from whom I have sought advice. A special thanks to my wife, Bonnie, for her help and understanding.

Financial assistance received from National Research Council of Canada is sincerely appreciated.

TABLE OF CONTENTS

	Page
LIST OF TABLES.	v
ABSTRACT.	vii
INTRODUCTION.	1
LITERATURE REVIEW	5
Crossability of Wheat and Rye.	6
Chromosome Doubling Techniques	7
Genetic Constitution of Hexaploid versus Octoploid Triticale	8
Fertility.	9
Seed Shrivelling	13
Protein.	15
Yield Components	17
Plant Characteristics.	20
1. Number of Spikes per Plant	21
2. Spike Length	22
3. Number of Spikelets per Spike.	23
4. Kernel Weight.	24
5. Kernel Colour.	24
6. Plant Height	25
7. Grass Dwarfing	28
8. Days to Heading.	29
9. Flag Leaf Measurements	30
General Combining Ability.	31
MATERIALS AND METHODS	34
Sources of Material.	34
Production of Experimental Material.	36
Experiments and Analyses	39
Plant Characteristics Measured	42
Growth Conditions.	43
RESULTS	46
Synthesis Techniques	46
Grass Dwarfing, Pericarp Colour, and 'Snoopy' Rye.	49
1. Grass Dwarfing	49
2. Pericarp Colour.	51
3. 'Snoopy' Rye	52

Interrelationships Among Rye Lines.	54
1. Variance Components	54
2. Correlations Between Environments	61
3. Correlations Between Inbred and Top-Cross Rye.	64
4. Correlations Among Characters of Inbred Rye	64
5. Correlations Among Characters of Top-Cross Rye.	69
Interrelationships Among Triticale Lines.	73
1. Variance Components	73
2. Correlation Among Characters of Hexaploid Triticale.	83
3. Correlation Among Characters of Octoploid Triticale.	85
DISCUSSION	88
Synthesis Techniques.	89
Grass Dwarfing and Pericarp Colour.	91
1. Grass Dwarfing.	91
2. Pericarp Colour	92
Variance Components	93
Environmental Effects	94
Correlations Between Inbred and Top-Cross Rye	96
Correlations Among Plant Characteristics.	97
1. Days to Heading	98
2. Plant Height	99
3. Flag Leaf Length.	100
4. Spike Number and Dry Weight per Plant	100
5. Spike Length and Florets per Spike.	101
6. Florets per cm.	102
7. Kernels per Spike, Fertility, Grain per Plant, and Harvest Index	102
8. Kernel Weight	103
9. Straw Protein	103
10. Grain Protein	104
CONCLUSION	105
Variance Components	105
Environmental Effects	106
Correlations Between Inbred and Top-Cross Rye	107
Correlations Among Plant Characteristics.	107
Relationship Between Rye and Triticale Amphidiploids.	109
LIST OF REFERENCES	110
APPENDIX	120

LIST OF TABLES

Table	Page
1. Identification and seed characteristics of rye lines (<u>S.cereale</u>), chosen for study.	35
2. Results of crosses between tetraploid wheat cultivar, 'Jori', and fourteen rye lines	47
3. Results of crosses between hexaploid wheat cultivar, 'Sonora 64', and fourteen rye lines.	48
4. Comparison of aqueous colchicine solution versus aqueous colchicine solution plus surfactant (dimethyl sulfoxide) on the doubling frequency of tetraploid and hexaploid wheat-rye hybrids	50
5. Segregation pattern of pericarp colour in inbred rye lines 194 and 100 in the growth cabinet and field experiments.	53
6. Mean square values and significance from the analysis of variance of fifteen plant characteristics for the <u>inbred rye lines in the growth cabinet experiment</u>	56
7. Mean square values and significance from the analysis of variance of fifteen plant characteristics for the <u>top cross rye lines in the growth cabinet experiment</u>	57
8. Mean square values and significance from the analysis of variance of the twelve plant characteristics on which individual plant data were recorded for <u>top-cross rye lines in the field experiment</u>	58
9. Mean square values and significance from the analysis of variance of the plant characteristics on which individual plant data were recorded for <u>top-cross rye lines in the field experiment</u>	59
10. Correlation coefficients between growth cabinets and between growth cabinet and field experiments for the inbred and top-cross rye lines	62
11. Correlation coefficients between inbred and top-cross rye lines grown in the growth cabinet and field experiments.	65

Table	Page
12. Simple phenotypic correlation coefficients between pairs of characters for nine parental rye lines grown in the field.	66
13. Simple phenotypic correlation coefficients between pairs of characters for ten parental rye lines grown in the growth cabinet	67
14. Simple phenotypic correlation coefficients between pairs of characters for nine top-cross rye lines grown in the field.	70
15. Simple phenotypic correlation coefficients between pairs of characters for nine top-cross rye lines grown in the growth cabinet	71
16. Mean square values and significance from the analysis of variance of the plant characteristics for the hexaploid and octoploid triticales lines . .	75
17. Mean square values and significance from the analysis of variance calculated on the means of each line for seven hexaploid and five octoploid triticales families.	76
18. Mean square values and significance from the analysis of variance of the plant characteristics for the hexaploid triticales data within each family.	77
19. Mean square values and significance from the analysis of variance of the plant characteristics for the octoploid triticales data within each family.	80
20. Simple phenotypic correlation coefficients between pairs of characters for the twenty-one hexaploid triticales lines grown in the growth cabinet	82
21. Simple phenotypic correlation coefficients between pairs of characters for the twenty-seven octoploid triticales lines grown in the growth cabinet	86

ABSTRACT

May, Kenneth William. Ph.D., The University of Manitoba, November, 1976. A Study of the Relationship and Performance of Parental Rye Lines, Their Top-Crosses, and Their Triticale Amphidiploids. Major Professor: Dr. E. N. Larter.

Successful plant breeding endeavours are dependent upon a broad genetic base from which superior genotypes may be selected. In the synthesis of triticale (X Triticosecale Wittmack) the production of new amphidiploids is the most common means of combining the genetic variability of the established wheat and rye species. However, the synthesis techniques presently available are not very efficient. One method of overcoming this inefficiency is by concentrating only on those wheat-rye crosses which are the best combiners. The objective of the present study was to investigate the effect of rye upon the plant characteristics in the top-cross rye hybrids and wheat-rye hybrids.

Mainly inbred parental rye lines were selected for this study because of their greater genetic homozygosity than cross pollinated rye lines. The parental rye lines were crossed onto Secale cereale, cultivar 'Prolific,' Tritium durum, cultivar 'Jori,' and Triticum aestivum, cultivar 'Sonera 64.' The crossing produced top-cross rye lines, hexaploid triticale lines, and octoploid triticale lines.

The results of the analyses of variance indicated that there was genetic variability within the inbred rye, top-cross rye, hexaploid triticales, and octoploid triticales. Thus, selection for all of the plant characteristics would be possible. The variation among hexaploid triticales lines occurred both within and between triticales families. The variation between these families was attributed to the difference between parental rye lines. Thus, a definite portion of the variation among the hexaploid triticales arose from the differences between parental rye lines.

The results of the analysis of variance of the field experiment indicated that four rye characteristics (the number of florets per spike, the number of kernels per spike, flag leaf length, and spike fertility) were not affected by the environmental differences occurring between the replications. The results of the correlations between the field and growth cabinet conditions showed that seven rye characteristics (the number of florets per spike, the number of kernels per spike, spike fertility, days to heading, harvest index, kernel weight, and straw protein) maintained consistent rankings, relative to one another. The phenotypic expression of the parental rye lines for six of the seven characters (excluding days to heading) was positively correlated with the expression of that character in top-cross rye. These six rye characteristics were genetically correlated between inbred and top-cross, and environmentally stable enough to be the basis of selection

of parental rye lines for hybridization.

The characters measuring grain production on a spike basis (number of kernels per spike and fertility), and harvest index were intercorrelated among the inbred rye, top-cross rye, and hexaploid and octoploid triticales. Straw protein was negatively correlated with most of these characters in rye and triticales. An additional negative correlation was obtained between days to heading and the characters measuring grain production in growth cabinet experiment with inbred rye and hexaploid triticales.

There were significant correlations among spike number, plant height, dry weight per plant, and spike length which were environmentally unstable characters among the rye lines. These significant correlations were present in many rye and triticales experiments but were not consistently correlated with the characters measuring grain production. This separation of the plant characteristics into two groups may have been caused by their respective sensitivity to environmental conditions.

There were many other significant correlation coefficients (especially with days to heading) but these did not occur consistently across several or all of the experiments. A few of the plant characteristics were conspicuous by their lack of correlations with other characters. The most notable of these were kernel weight, grain protein, and the number of florets per spike.

The intercorrelations among the characters measuring

grain production and plant development means that only one character need be measured to represent each trait. The characters measuring grain production (kernels per spike, fertility, and harvest index) were environmentally stable and contained significant correlation coefficients for the studies between inbred and top-cross rye. The intercorrelated characters measuring plant development (spike number, dry weight per plant, and plant height) were not environmentally stable and were not consistently correlated between inbred and top-cross rye. These characters would not be very reliable as selection indices under the present conditions of experimentation. Kernel weight and the number of florets per spike would each prove to be good selection indices because of their non-significant correlation with other characters, environmental stability, and correlation between inbred and top-cross rye lines. Selection among the present rye lines for one of the characters measuring grain production (kernels per spike, fertility, or harvest index), kernel weight, and florets per spike would produce more desirable triticales than if selection had not been applied. The improvement in the triticales would occur in characters for which selection was practiced.

INTRODUCTION

Triticale (X Triticosecale Wittmack) is a recently developed species and consequently still has a narrow genetic base. As this base is broadened due to breeding, selection, and utilization of an increasing array of parental species of wheats and ryes, certain agronomic problems inherent in early triticales are gradually being overcome. Gustafson (1973) outlined techniques being used to increase the variability within the triticale species. These techniques are:

- (1) synthesis of new amphidiploids,
- (2) 56- X 42-chromosome triticale crosses,
- (3) tetraploid wheat X 42-chromosome triticale crosses,
- (4) diploid rye X 42- or 56-chromosome triticale crosses,
- (5) hexaploid wheat X 42- or 56- chromosome triticale crosses,
- (6) 42-chromosome agrotriticum X 42-chromosome triticale crosses,
- (7) 42-chromosome triticale X 42-chromosome triticale crosses,
- (8) screening composite populations mainly to select specific phenotypes (large seed types).

The synthesis of new amphidiploids is the only technique of the eight listed by Gustafson (1973) which brings an entirely new rye genome into triticale. This technique is the most common method for bringing new genetic variability from rye species into triticale. However, there are a

couple of major disadvantages associated with the synthesis of new amphidiploids. It is the most difficult technique because it requires lengthy and involved processes in the laboratory. In contrast, the other techniques can all be accomplished in the field. The second disadvantage is that the new amphidiploids will have more numerous meiotic and/or agronomic abnormalities than the recombinants from the other techniques. This situation exists because the parental triticales material used in the other techniques listed by Gustafson (1973) has already been selected to remove many of the undesirable characters.

The efficiency of the production of desirable raw amphidiploids may be improved considerably if the selection and/or predictive tests suggested by Kaltsikes (1974) and Darvey (1973) could be conducted on the parental rye before synthesis of the new amphidiploids. McDaniel (1973) has suggested the use of mitochondria complementation test to select the lines of rye and wheat which appear to offer potential for triticales synthesis. The extension of this type of parental testing to plant and grain characteristics has not been reported in the literature. There is a lack of information on rye species concerning the genetics of agronomic characteristics and their contribution to the genetic background of triticales. Heritability studies have been extensive in wheat and limited in rye and triticales. Thus the information from wheat must generally form the basis for the assumptions concerning the genetics of agronomic characteristics in

rye and triticales.

Another important question concerning triticales synthesis, is the influence of the parental rye on the resulting triticales. In a study by Quinones et al. (1972) it was shown that resistance to wheat leaf rust (Puccinia recondita), in the rye parent was not transferred to the resulting triticales. However, Morrison (1975) found that wheat stem rust resistance, Puccinia graminis tritici, was transferred from rye to triticales. The need to determine the importance of the rye parent to the agronomic and reproductive characteristics of the triticales formed the basis for the present study.

The objective of the present study was to investigate the effect of rye characteristics upon the respective characteristics in the top-cross rye hybrids and wheat-rye hybrids. Statistical analyses were performed on the data from top-cross rye, hexaploid triticales, octoploid triticales as well as the parental rye lines. Information about individual characters was obtained from rye and triticales by conducting correlations between the data from each pair of plant characteristics and an analysis of variance upon the data for each character in each experiment. Additional information about each character within the rye lines was obtained from correlations between growth cabinet and field conditions as well as between inbred and top-cross lines of rye.

In addition to the main objectives outlined above, the method and effectiveness of amphidiploid synthesis was also evaluated in respect to the triticales produced for

this study. Similarly, the inheritance of pericarp colour and grass dwarf hybrids as they related to the rye and triticale in this study, was also studied.

LITERATURE REVIEW

This literature review is presented in the following nine sections: 1. a summary of the factors controlling crossability,

2. a review of the chromosome doubling techniques pertinent to the present study,

3. a short discussion of the relationship of ploidy level as it relates to the agronomic and biological behaviour of triticales,

4. a discussion of meiotic stability and its relationship to grain yield,

5. a review of the studies attempting to explain the cause of seed shrivelling in triticales,

6. a brief summary of the inheritance of grain and plant protein,

7. a review of the literature concerning yield components in small cereals,

8. a summary of the inheritance and correlations among plant characteristics,

9. a review of the studies of general combining ability in relationship to hybrid production and application to triticales synthesis.

Crossability

Crossability of wheat and rye is genetically controlled by two major genes located on chromosome 5A and 5B (Riley and Chapman, 1967). Highly crossable wheats produced approximately 50% seed-set and the low crossable wheats 5% or less (Riley and Chapman, 1967; Kaltsikes, 1974). Riley and Chapman (1967) concluded that tetraploid wheats more readily set seed when crossed with rye than almost all of the hexaploid wheats of Europe that he tested. The crossability indicated by the percent seed-set presented by Kaltsikes (1974) illustrated the great variation among tetraploid and hexaploid wheats in their crossability with rye. The data presented by Krolow (1970) indicated that the majority of the forty-six varieties in six species of tetraploid wheat tested were in the mid and high crossability categories. The very low natural germination of these tetraploid embryos was attributed to abnormalities in embryo and endosperm development. The seed-set of 4.96% given by Krolow (1970) for hexaploid wheat when crossed with rye was lower than his values for tetraploid wheat. However, the germination of the hybrid seed from hexaploid wheat was 61.83% which resulted in a higher percentage of hybrids in comparison to those from tetraploid wheat.

In a series of investigations, Tozu (1966) searched for the physiological stage at which the genetic crossability factors have their effect, and narrowed the phenomena to a period either directly before or after fertilization. The stigmatic receptivity of wheat and the pollen tube growth of

rye in the wheat style was not affected by the crossability genes.

The theory has been advanced by Riley and Chapman (1967) that crossability genes could have developed to prevent wheat from naturally crossing with rye and producing its own weeds. Kaltsikes (1974) concluded that the specific genetic factors preventing the crossing between wheat and rye developed gradually. This conclusion was based upon the fact that crossability between tetraploid wheat and primitive rye was higher than with cultivated ryes (Kaltsikes, 1974).

Chromosome Doubling Techniques

The alkaloid colchicine is the most commonly used chemical to induce doubling in triticale hybrids. Kaltsikes (1974) briefly reviewed nine methods by which colchicine can be applied and the degree of success experienced with each of the methods. The most effective and commonly used was the capping method proposed by Bell (1950). One or more tillers are cut back to 2-3 cm in length and a vial containing a 0.2 - 0.3% aqueous solution of colchicine is inverted over each cut tiller for seventy two hours. Sanchez-Monge (1958) reported a doubling rate of forty-six percent using the capping method for embryos produced from hexaploid wheat and diploid rye. Using this method he applied colchicine to one to three tillers on plants containing four to eight tillers respectively.

The effectiveness of the colchicine treatment has been increased three to four times by using the surfactant dimethyl

sulfoxide (Sanders and Hull, 1970; Subrahmanyam and Kasha, 1975). Sanders and Hull (1970) obtained an increased rate of doubling from the solution of colchicine and dimethyl sulfoxide when applied to germinating seeds of *Rubus*, but no effect when applied to the apices. The barley haploids used by Subrahmanyam and Kasha (1975) were doubled at the 2- or 3-leaf stage in a culture vial. A 3-4 ml solution, which covered the crown, was poured into the vial and left for five hours before washing the plant and potting it in soil.

Genetic Constitution of Hexaploid versus Octoploid Triticale

Various combinations of the genomes from Gramineae have been produced for research purposes in an attempt to produce new and improved species (eg. triticale). Genome inter-relationship and combining ability was investigated in relation to its effect on yielding capacity (Shebeski, 1958). The research presented by Shebeski (1958) indicated that the R genome of *Secale cereale* was a better combiner than the D genome of *Aegilops squarrosa* L. with the A and B genomes of tetraploid wheat. Manipulation of whole or parts of genomes may produce a genotypic combination with improved yielding capacity compared to the present species.

The first triticales synthesized by man were between hexaploid wheat and diploid rye (Muntzing, 1939). Emphasis then shifted towards the use of tetraploid wheat parents because of the improvement in seed-set, fertility, and

genetic stability of the hybrids (Larter et al., Muntzing, 1972). More recently, the extracted A and B genome from hexaploid wheat in hexaploid wheat cytoplasm has been crossed with diploid rye to produce hexaploid triticales. Sisodia and McGinnis (1970) have expressed the opinion that hexaploid wheat cytoplasm should produce improved hexaploid hybrids because it has been adapted to accepting alien genomes and it has become preadapted to operating with three genomes.

Fertility

The interrelationship of fertility or seed yield and meiotic disturbances has been extensively investigated in triticales. A positive relationship existed between fertility and meiotic disturbances during the early generations after the production of the primary triticales but this correlation disappeared with advancing generations (Rupert et al., 1973; Hsam and Larter, 1973). Tsuchiya (1972a) suggested that meiotic abnormalities will affect the yield up to a certain threshold value. Other studies have shown that although meiotic instability may exist there was no apparent relationship between this characteristic and low fertility (Riley and Chapman, 1957; Merker, 1971 and 1973b; Boyd et al., 1970; Kampanna and Seetharam, 1972). A positive relationship has been reported between meiotic irregularities and the frequency of aneuploids in the following generation (Merker, 1971). Aneuploid plants are less fertile and less vigorous than corresponding euploid plants and must be avoided if maximum yields

are to be obtained (Merker, 1973b). Aneuploid plants have also been associated with reduced seed size (Tsuchiya, 1972; Weimarck, 1975).

The cause of meiotic instability has been attributed to the loss of rye chromosomes from octoploid triticales (Muntzing, 1939). The univalents were assumed to arise exclusively from the rye genome because of the tendency for octoploid triticales to revert to wheat and the common occurrence of univalents when out-crossed rye was inbred (Muntzing, 1939, and 1963). Sanchez-Monge (1958) reasoned that the univalents which appeared in his octoploid and hexaploid triticales were from the rye genome because the univalents appeared in equal frequency at both ploidy levels. Inbreeding depression in the rye genome has also been cited as a possible cause for the preferential loss of rye chromosomes in octoploid triticales (Muntzing, 1939). Recent studies by Shigenaga et al. (1971), Larter and Shigenaga (1971), and Merker (1973a) have shown very clearly that both rye and wheat chromosomes are lost from triticales. These studies were all based on chromosome measurement by which wheat and rye chromosomes can be identified with reasonable accuracy.

Disturbances in meiotic stability in triticales have been shown by Bennett and Kaltsikes (1973) to be affected by the different meiotic rates of the parental species wheat and rye. The rye cultivar, 'Prolific,' had a longer meiotic time than the tetraploid wheat cultivar, 'Stewart.' The resulting triticales was intermediate in its length of time to complete

meiosis but closer to that of the wheat parent. Recently, Roupakias and Kaltsikes (1976a and b) have shown that no relationship exists between duration of meiosis and the degree of chromosome pairing in triticales.

Mitotic cycles were shortest in rye and longest in wheat (Kaltsikes, 1971) but Bennett (1973) does not consider these great enough to cause aneuploidy. Kaltsikes (1972) also has shown a difference in the mitotic cycle of the triticales 'Rosner' and 'Armadillo' which he attributed to the background material used to develop these varieties.

The self compatability characteristic present in some lines of diploid rye has received a great deal of attention in regards to its possible effect on fertile and meiotically stable triticales. Muntzing (1957) was the first to suggest that inbred rye rather than open-pollinated rye would produce the best primary triticales. He reasoned that the normal inbreeding depression observed in rye occurred in triticales produced from cross-pollinated rye. Riley and Chapman (1957) suggested that lines of rye adapted to inbreeding would produce triticales with fewer deleterious interactions between the genotypes of rye and wheat. Muntzing (1963) obtained a wide range of triticales from inbred rye and concluded that selection among these triticales could produce lines better than if out-crossed rye had been used in the initial crosses. However, Weimarck (1973) obtained a higher frequency of aneuploid plants when self fertile rye was used to produce

triticale. Merker (1973e) concluded that inbreeding and homozygosity of the rye chromosomes in triticale could not be considered the only cause of meiotic irregularities. These conclusions were based upon the fact that the meiosis was more disturbed in F1 triticale hybrids than in either of their parental triticales. These results may be attributable to genetic changes which could have occurred in the rye genome thus preventing complete chromosome pairing when the genomes are brought together in the F1 triticale hybrid.

The significant differences in meiotic irregularities and fertility in eight lines of triticale has led Merker (1971) to conclude that the genetic factors affecting fertility and meiotic irregularities are independent. These results supported a suggestion by Muntzing (1939) that meiotic irregularities and partial sterility were separate phenomena which extend from a common physiological disturbance.

Rupert et al. (1973) were able to increase the number of seeds per spikelet by 66.9% in three generations after the synthesis of hexaploid triticale by selecting for meiotic regularity and plant type. Fertility in wheat has been shown to be controlled by a minimum of five genes (Halloran, 1974) and if extended to triticale it may explain the improvements in seed-set which are possible immediately after synthesis by selection. Merker (1971) concluded from his and other work that recombination and selection would considerably improve fertility and stabilization of meiosis in early generation triticales.

In a study by Gebremariam (1974), the wheat cultivar 'Glenlea' was found to be superior in seed-set to all of the advanced strains of triticale tested. The number of kernels per spikelet and kernels per spike, which were used as a measure of fertility, showed positive correlations with grain yield, spike length, days to heading, and plant height as well as negative correlations with tillers per plant, kernel weight, and grain protein. Gustafson et al. (1975) found that fertility was positively correlated with yield per plant and kernels per spike in an F₃ population of hexaploid triticale. Results from winter wheat (Fonseca and Patterson, 1968) and spring wheat (Hsu and Walton, 1970 and 1971) all indicated a positive correlation between kernels per spike and grain yield. The number of kernels per spike was found to be highly heritable (Fonseca and Patterson, 1968) and a large part of its genetic variation was from additive genetic effects in wheat. Grain yield per plant has been found to be highly heritable in hexaploid triticale (Sethi and Singh, 1972). The results of these studies indicated the possibility of improving the level of performance of new triticale lines by selecting for fertility and plant yield.

Seed Shrivelling

Seed shrivelling, which manifests itself as low seed weight and poor seed appearance, has been a major problem preventing the production of high quality triticale grain. However, rigorous selection has reduced the amount of

shrivelling (Zillinsky and Borlaug, 1971) and caused the percentage of starch to increase at the expense of protein percentage (Zillinsky, 1973a).

Physiological examination of shrivelled triticale grain has shown a precocious release of amylase (Klassen et al., 1971; Shealy and Simmonds, 1973). Klassen et al. (1971) reported normal development of shrivelled triticale lines until 55% moisture was reached at which time amylase continued to build up and starch deposition was stopped.

Hill et al., (1973) utilized sucrose ^{14}C feeding to determine that cultivars with shrivelled seed transport sugars more slowly and less efficiently to the grain than cultivars with non-shrivelled seed. However, Fischer (1973) used leaf removal and plant thinning studies which indicated that the photosynthate translocation system was probably not limiting in triticale cultivars with shrivelled seed. Fischer (1973) believed that seed shrivelling represented a genetic limitation in the sink capacity.

Shealy and Simmonds (1973) and Dedio et al. (1975) observed that the endosperm and aleurone regions were the main tissue affected by seed shrivelling. The shrivelling characteristic has been isolated by Darvey (1973) to factors carried on rye chromosome 4R/7R, 5R, and 6R and on wheat chromosomes 5A and 6B. 3R has shown some effect on seed shrivelling in the cultivar 'Rosner.'

Protein

Most of the literature concerned with protein content and its inheritance in small seeded cereals is on wheat. Grain protein content has been shown to be quantitatively inherited and influenced by the environment. Johnson et al. (1974) found the average protein content of wheat grain to be approximately 12% with the range of 6 to 22% in a survey of the world collection of bread and durum wheats. These authors felt that most of the variations in seed protein was non-genetic and only a response to the environment. Partial dominance for low grain protein in wheat has been reported by Davis et al. (1974) while Kaul and Sosulski (1975) could not find any net dominance for low or high grain protein. The inheritance of straw protein content in oats had indicated additive gene action (Campbell and Frey, 1974). The straw protein content of oats was positively correlated with heading date but not with plant height, percent groat protein, or ten groat weight.

The percentage of protein in wheat grain has been found to be negatively correlated with the quantity of grain protein (Hsu and Sosulski, 1969; McNeal et al., 1972). However there was a positive correlation between grain yield and the amount of grain protein in grams (McNeal et al., 1972). Although the percentage of protein was decreased with increased yields the overall yield of protein in grams was increased.

A considerable amount of variation exists in the

relationship of plant and grain nitrogen contents. The lines of wheat selected for high grain protein by Johnson et al. (1967) contained a higher nitrogen content throughout the period of grain development than those lines which had a low grain protein. There was no significant difference in grain yield between the high and low protein lines. The line of wheat which had the highest straw protein also contained the lowest grain protein. The authors concluded that this line had a good ability to take up nitrogen from the soil but a poor ability to translocate the nitrogen to the grain. Wheat plants of a high grain protein selection contained the lowest level of plant nitrogen. The authors concluded that there was a good nitrogen translocation to the grain and a poor nitrogen uptake from the soil. In contrast, a study by McNeal et al. (1972) could find no differences in plant nitrogen content, straw nitrogen yield, or nitrogen translocation between lines of wheat which had been selected for high and low grain protein. The differences in grain protein were attributed to the lower test weight and the smaller number of kernels per spike of the high protein selections.

The results presented by Plarre and Fischer (1975) in rye indicated that the protein was mainly located in the aleurone layer. The percentage of protein in rye increased as the seed size decreased. The protein content was also shown to be influenced by the environment. A diallel cross of six inbred rye lines indicated that a low protein content was inherited due to the accumulation of dominant alleles.

A study with hexaploid triticale was conducted by Gebremariam (1974) in which the protein content was compared with fourteen other plant and grain characteristics. Protein was positively correlated in hexaploid triticale with tillers per plant and test weight as well as negatively correlated with kernels per spike, kernels per spikelet, maturity, plant height, lysine, and grain yield.

Triticale provides an opportunity for plant breeders to increase the amount of protein in a cereal grain. New amphidiploids contain high protein levels but as the kernel types of these hybrids is improved protein percentage decreases. Present triticale protein levels are approximately 15.0% on a 14% moisture basis and a 5.7 conversion factor which is approximately two units above the standard bread wheat (Larter, 1973).

Yield Components

Many attempts have been made in plant breeding to select specific yield components or a combination of components to be used as selection criteria for yield. The correlation and heritability studies of yield and its components have revealed some of the complexities involved in their inheritance. Correlation studies in spring and winter wheat (Hsu and Walton, 1970; Fonseca and Patterson, 1968) have shown positive correlations between yield and the components of yield (spike number, kernels per spike, and 1000 kernel weight). Although yield and components of yield are positively correlated the components of yield themselves are

negatively correlated. Many studies have been implemented to explain the relationship between yield and its components and the interrelationship among the components of yield.

Grafius (1956) represented yield as the volume of a rectangular parallelepiped with the components of yield (panicles per unit area, average number of kernels per panicle, average kernel weight) as the length of the sides. Yield could most easily be increased by extending the shortest side of the parallelepiped.

The interrelationship of yield components among themselves and with yield has been described by Adams (1967) as a response to the amount of metabolites available. When metabolites are plentiful and/or competition is low the yield component developing at that time is increased and vice versa. An increase in a yield component which develops early will exert greater pressure on later developing components by greater competition or reduced metabolites. This type of compensation exists only within a certain range. Jones and Hayes (1967) reported that the medium and high seeding rates in oats yielded the same but higher than the low seeding rate. The reduced plant numbers in the low seeding rate could not produce sufficient increases in the other yield components to attain the yield of the other two seeding rates.

Selection for one yield component can improve or depress the grain yield. Nickell and Grafius (1969) doubled the number of spikes per plant and their results showed reductions in kernels per spike, kernel weight, and grain

yield. The yield decrease indicated that the intense selection to increase spike number (136 lines out of 387 lines) could not compensate for the reductions in kernels per spike and kernel weight. In barley, effective selection for kernels per spike reduced the overall yield (Rasmusson and Connell, 1970). Each of the effects reported by Rasmusson and Connell (1970) occurred in only one of two populations of barley. Knott and Talukdar (1971) reported a successful increase of seed weight in Thatcher by transferring a large seed character from 'Selkirk' through a back-crossing program. The seed weight was increased by 19% and the yield was increased by 6%. In this case the genetic increase in one component was not completely lost due to the compensatory effect of the other components of yield. Fonseca and Patterson (1968) pointed out that selection for components of yield is most effective when the components are highly heritable, when the components are genetically independent, and when there is no physiological association among the components.

Recent attempts to explain yield component interactions have been based upon plant requirements and the resources available to meet these requirements. Adams (1967) and Grafius (1972) envisioned the different components of yield being drawn from a common resource pool. Negative correlations would occur between genetically independent components of yield which are drawing upon the resource pool at the same time thus creating competition among the character traits. Grafius (1972) observed that competition within

character traits was more intense than between different character traits. This occurred because the units of the same character demand metabolites at the same time whereas different characters may require metabolites at different times during plant development. The more intense competition within character traits was chiefly responsible for the stability of the thirty-six lines of wheat over three environments. A high component mean has been interpreted by Grafius (1972) as a relatively higher competitive ability within and between components.

A formula or set of yield components have often been sought as a more efficient alternative to yield improvement than just yield itself. Nass (1973) conducted a study with spring wheat to determine which characters would be most effective for increasing the yield. The results suggested that spike number per plant, yield per spike, and harvest index considered collectively would be the best combination of yield components for use in a selection program for yield improvement.

Plant Characteristics

Plant breeding for increased yield requires an understanding of yield component interaction as well as the type of gene action associated with each component. The type of gene action associated with plant characteristics is reviewed in the following section. The literature is primarily concerned with wheat and is used to indicate the type of gene

action which occurs and which may be similar to the situation present in rye and triticale.

The spike characteristics, especially those determining sink capacity, are generally correlated with grain yield. Predominantly, additive gene action with some dominance effects has been reported in most references (Lee and Kaltsikes, 1972; Chapman and McNeal, 1971) for spike characteristics. However, Amaya *et al.* (1972) observed dominance to be the most important type of gene action affecting yield in durum wheat. Epistatic gene action for yield is either absent (Lee and Kaltsikes, 1972) or inconsistent (Chapman and McNeal, 1971) in wheat.

1. Number of Spikes per Plant

The number of spikes per plant is one of the three yield components generally considered to be the most important in determining yield. Hsu and Walton (1971) and Sethi and Singh (1972) found spike number to be the most important yield component in spring wheat and in hexaploid triticale. Gene action determining spike number in durum wheat was found to be predominantly additive with some degree of dominance but with a lack of epistatic gene activity (Lee and Kaltsikes, 1972). Sethi and Singh (1972) found that the number of spikes per plant of hexaploid triticale was highly heritable.

Numbers of tillers and spikes per plant were found to be correlated with plant and plot yield in spring rye (Kaltsikes, 1973a). Fischer (1973) reported that triticales

generally have a lower spike number than most bread wheats of the same maturity and both increased with increasing maturity dates. Tiller survival at the various maturity dates was lower in triticale than in wheat. Number of tillers per plant was found to be negatively correlated with kernel number per spike, plant height, and yield per plot in hexaploid triticale (Gebremariam, 1974). Spike number is an important component of yield and will likely respond to selection in triticale because of the predominantly additive gene action.

2. Spike Length

Spike length has been shown to have an influence on yield and other yield components in wheat. Hsu and Walton (1971), Zitelli and Mariani (1973), and Johnson et al. (1966a) found that inheritance of spike length in wheat was controlled by only additive gene action. Fischer (1973) and Larter (1973) both indicated that increased spike length in triticale lines would likely lead to higher yields.

Some triticales spend a longer period of time in spikelet initiation than bread wheat (Fischer, 1973). This spike development pattern is a unique feature of triticale and may offer an important means of increasing yields beyond those of other cereals. Fischer (1973) compared the spike development pattern of a Norin 10 wheat derivative and wheat with a normal stature. The semi-dwarf line had a different pattern of ridge development, a longer and slower rate of

development, a larger final spikelet number, and an improved fertility. Fischer (1973) found that the spike development pattern of semi dwarf wheat was similar to rye.

A triticale study in which simple correlations were used indicated that spike length was positively related to number of kernels per spike, days to heading, plant height, and plot yield (Gebremariam, 1974). Spike length was negatively correlated with kernel weight and grain protein in hexaploid triticale (Gebremariam, 1974). In contrast to the previous study Sethi and Singh (1972) found spike length to be positively correlated with kernel weight in the 31 strains of hexaploid triticale. Spike length is an important character in triticale not only because of its relationship to yield and additive variance but also because of its unique developmental pattern.

3. Number of Spikelets per Spike

The number of spikelets per spike is determined predominantly by additive gene action in wheat (Chapman and McNeal, 1971; Johnson et al., 1966a; Lee and Kaltsikes, 1972). A minimum of six genes affected the expression of spikelet number per spike in wheat (Halloran, 1974). Spikelet density in wheat was shown by Kuspira and Unrau (1957) to be controlled solely by minor genes. In conclusion, spikelets per spike and spike density are controlled by only a few genes and should prove responsive to selection in triticale.

4. Kernel Weight

Kernel weight in wheat is controlled primarily by additive gene action with smaller effects due to dominance (Chapman and McNeal, 1971; Sun et al., 1972; Bhatt, 1972; Lee and Kaltsikes, 1972; Ketata et al., 1976). Johnson et al. (1966a) concluded that kernel weight was determined by only a few genes in wheat while Kuspira and Unrau (1957) indicated it was controlled by many genes.

Kernel weight was positively and significantly correlated with number of kernels per spike, plant yield, and plot yield in spring rye (Kaltsikes, 1973a). Kernel weight has been shown to be negatively correlated with number of kernels per spike, spike length, days to heading, and plant height in hexaploid triticale (Gebremariam, 1974). Sethi and Singh (1972) also found kernel weight negatively correlated with days to heading. Kernel weight was highly heritable in hexaploid triticale (Sethi and Singh, 1972). Kernel weight may prove to be an important characteristic in triticale because of its relationship to yield and simple inheritance.

5. Kernel Colour

Several different kernel colours have been reported in wheat and most appeared to exhibit simple inheritance patterns. Sharman (1958) reported a purple coloured tetraploid wheat of Abyssinian origin. The purple pericarp condition was inherited as a simple monofactorial dominant. Purple coloured hexaploid wheat has also been reported by

Copp (1965) which faded during back-crossing but was restored when crossed to a normal red wheat. Knott (1958) and Hurd (1959) observed blue endosperm colouring in Agropyron. The inheritance in both cases appeared to involve only a few genes.

Watkins et al. (1964) reported a complementary gene inheritance pattern for the blue anthocyanin pigmentation of the aleurone layer in selections from rye cultivar 'Prolific.' Complementary gene action was also observed in earlier studies (Watkins et al., 1964) but the results of the earlier studies indicated independent segregation. Watkins et al. (1964) observed a 5.6% linkage between the two complementary genes. Pericarp pigmentation is not likely to become an important character in triticales but it may serve as an excellent character for inheritance studies between the parental species and triticales.

6. Plant Height

New triticales amphidiploids produced from wheat and rye germplasm available in Manitoba are generally vigorous and tall (Zillinsky and Borlaug, 1971). Breeding endeavours have been directed towards shortening the height of the triticales. This aim can be advanced through the use of the day-light insensitive semi dwarf lines of wheat.

Culm length in normal height wheat has a complex inheritance pattern. Kuspira and Unrau (1957) found genetic factors affecting height on eight of the twenty-one pairs of

chromosomes in wheat while Allan and Vogel (1963) found genetic factors on eleven of the twenty-one pairs of chromosomes. In contrast, Halloran (1974) detected a minimum of three genes affecting plant height in a cross between Chinese Spring and the winter wheat variety 'Hope.' Johnson et al. (1966a) also detected three genes affecting plant height in the progeny from the cross between 'Seu Seun 27', a short variety, and 'Blue Jacket', a tall variety.

Allan et al. (1968) reported the same pattern of genetic control for semi dwarfness in each of three varieties studied. Generally there were two major genes and several minor genes controlling semi dwarfness. Fick and Qualset (1973a) observed four independently segregating loci and mainly additive gene action in crosses between a normal stature and three semi dwarf wheats. Romero and Frey (1973) obtained partial dominance for tallness over semi dwarfness in all crosses between normal and semi dwarf wheats. These authors determined that 'Sonora 64' differed from wheat of normal stature at only one locus affecting plant height.

Many authors (Johnson et al., 1966a; Amaya et al., 1972; Bhatt, 1972) have indicated that in wheat most of the variation in height was due to additive gene action. Ketata et al. (1976) however, found non-additive gene action in winter wheat.

A positive correlation has been observed between plant height and kernel weight (Reddi et al., 1969; Johnson et al.,

1966a and 1966b; Zittelli and Mariani, 1973). Semi dwarfness originating from Norin 10 has been found to be correlated with lower kernel weight, lower spike number per plant, higher kernel number per spike, longer spike, and higher yields. These correlations are not generally found among wheat varieties of normal stature (Johnson et al., 1966b; Reddi et al., 1969).

Short stature in the triticales may be introduced from the rye parent as well as the wheat parent. Kobylanski (1975) described a natural short rye mutant which was controlled by a single dominant gene in the homozygous condition. The height was decreased by 40% which increased the lodging resistance even with supplementary fertilization. The rate of morphological development of the plant was reduced but internode number and stem diameter or thickness was not affected. The spikes were significantly longer on the dwarf plant as a result of an increased number of spikelets. This dominant character for short straw does not have the usual negative associations with other plant characters that are common in other dwarf ryes. Another dwarf rye known as 'Snoopy' has been selected from an openpollinated population of the variety 'Gator' (Zillinsky, 1973c). A third dwarf rye, UC-90, has been described by Gustafson et al. (1973).

Plant height in hexaploid triticales has been positively correlated with kernels per spike, spike length, days to heading, and yield per plot (Gebremariam, 1974). Plant height has also been negatively correlated with kernel weight,

spike number, and grain protein in hexaploid triticales (Gebremariam, 1974). Sethi and Singh (1972) found plant height to be positively correlated with spike length and kernel weight in a study of 31 strains of hexaploid triticales. These authors also found plant height to be highly heritable.

Fisher (1973) has attributed, at least part of the increased yield in recent triticales, to their reduced plant height and improved harvest index. Plant height is often a genetically complex character but because of its relationship to yield it is a very important one.

7. Grass Dwarfing

Aestivum crosses have produced a low frequency of stunted hybrids which are different from the semi dwarf varieties. They have been referred to as grass dwarf, hybrid dwarf, or grass clump dwarfs. These plants differ from the common semi dwarf geneotypes in that they have a densely tufted grass-like habit and rarely flower, or flower very late under normal environmental conditions in the field (Moore, 1966). These plants may be induced to flower in the greenhouse if they receive direct sunlight, high temperatures, and Gibberellin A3 treatments of 100 ppm at 7 or 14 day intervals.

There is a specific physiological and genetical cause of grass dwarfness which is different from that of semi dwarfness (Hermsen, 1967) although each type may have originated from a common source (Fick and Qualset, 1973b). Researchers agree that this trait is simply inherited and generally

controlled by three genes (Hernsen, 1967; Moore, 1969; Hurd and McGinnis, 1958; and Fick and Qualset, 1973b). The presence of grass dwarfing in T. aestivum was first reported in the late nineteenth century (Fick and Qualset, 1973b) and its presence has been continually observed since then. Dwarfing genes have been located in semi dwarf wheat as well as wheat of normal stature (Fick and Qualset, 1973b). Grass dwarf mutants have also occurred in crosses among triticales lines (Salmon, personal communication).

8. Days to Heading

The number of days required for spike emergence is a criterion which has been used extensively in the study of inheritance of earliness in bread wheat. Some researchers, such as Johnson et al. (1966a), have found days to spike emergence to be controlled by only a few genetic factors. Another group of researchers have found multi-genic control of the number of days to spike emergence (Halloran, 1975; Kuspira and Unrau, 1957; Crumpacker and Allard, 1962).

Amaya et al. (1972), Bhatt (1972), and Ketata et al. (1976) determined that additive gene action in wheat was the most important factor in determining the number of days to heading. Halloran (1975) postulated the existence of two types of gene action, the first dealing with the initiation of heading and the second with the rate at which the plant progresses to spike emergence. The number of genetic factors determining the time required for spike emergence is variable

but because it is under additive gene control, selection for a shorter period to spike emergence may be successful in triticale.

9. Flag Leaf Measurements

Flag leaf measurements were made by Hsu and Walton (1971) which indicated that leaf sheath length and leaf breadth influenced the yield and yield components in wheat. Flag leaf length was associated with the number of kernels per spike and kernel weight but not with yield. The importance of the photosynthetic area of the spike and flag leaf have been shown by Voldeng and Simpson (1967) in wheat. Shading studies indicated that the photosynthetic activity of the flag leaf and spike contributed more to grain yield than the photosynthetic activity of the other plant parts. The photosynthetic area of the spike and flag leaf in spring wheat (Nass, 1973) was associated with yield per spike. These latter results were based upon correlations from a two year study involving twenty-two cultivars of spring wheat. In contrast, Kaltsikes (1973a) found no correlation between yield of spring rye and the characters of the flag leaf. The references concerning flag leaf characteristics, especially flag leaf length, are not plentiful but the importance of the flag leaf in photosynthesis and grain filling makes it an important character.

General Combining Ability

Early adoption of hybrid corn and its economic importance has generated a great deal of research into the identification of superior inbreds for hybrid production. In 1929, Jenkins stated that inbred lines of value for the production of double cross, multiple cross, and synthetic varieties are those which combine well with a large number of inbred lines. A varietal mixture or a single open pollinated variety was proven to be an adequate tester for general combining ability in corn inbred lines (Jenkins and Brunson, 1932). In a more recent study, (Nanda, 1966), eight inbred lines of corn were ranked the same when evaluated on the basis of (1) performance of the inbred line per se (2) top-cross performance when crossed with an open pollinated variety and (3) single cross performance when crossed with two test inbreds. The exclusive use of inbred line performance to evaluate hybrid performance has been successfully used in corn by Lonquist and Lindsey (1964) and Genter and Alexander (1966).

Reciprocal crossing between inbred lines and a broad base tester showed much less variation in seed-type and performance when the tester was used as the seed parent (St. John, 1934). The variance in the means of the samples from ten to twenty plants of an open pollinated seed parent tester has been shown to be less than the variance ascribed to random error (Sprague, 1939). Jenkins and Brunson (1932) concluded that the use of a broad base seed parent tester in the determination of general combining ability of potential corn

inbreds, was adequate to safely discard up to one half of the original material. Thus reliable general combining ability testing using top-cross material could be conducted if ten to twenty plants of a broad base tester were used as the seed parent.

As well as the type of tester, the time of testing has received extensive research attention in corn. Jenkins (1940) has shown that the use of top-crossing in corn at the S₀ generation allows only one chance in forty of selecting a plant that will give an S₁ line that is 8.9% better than the original variety. Sprague (1946) obtained significant differences among the top-crosses from S₀ plants and recommended early testing for characters with low gene frequency and those which can be evaluated easily. The potential of a plant to become a good inbred line is determined very early in the inbreeding process (Jenkins, 1935).

The potential of hybrid wheat has led to the initiation of studies to determine the heterosis and the combining ability of wheat. Kronstad and Foote (1964), Gyawali et al. (1968), and Brown et al. (1966) working with winter wheat all reached similar conclusions. They concluded that a large part of the total genetic variation for yield as well as the other yield components in winter wheat were associated with a significant general combining ability effect. Widnor and Lebsock (1973) determined that the general combining ability mean squares were highly significant among F₁'s and F₂'s for all of the nine characters studied in durum wheat. A large part

of the variation in oil content in oats was associated with general combining ability (Brown et al., 1974). These studies on winter wheat, durum wheat, and oats all involved a diallel analysis which permitted the determination of specific combining ability. These latter determinations showed small or non-detectable differences.

Morgenstern and Geiger (1975) reported at a conference in Poland on inbred rye line evaluation for the production of rye hybrids, that the top-cross test was sufficient for inbred line analysis until the final selection of inbred lines for hybrid rye production. This final evaluation required the calculation of specific combining ability as well as general combining ability. The top-cross evaluations by Morgenstern and Geiger (1975) with unselected inbred lines of rye showed that general combining ability accounted for most of the genetic variance between crosses. General combining ability estimates were the highest for plant height and lodging, intermediate for heading date and grain protein, and lowest for grain yield and kernel weight.

MATERIALS AND METHODS

Sources of Material

The bulk of rye parental lines for study were selected from the inbred lines made available by Dr. L. Evans. One rye line (accession number 2082-3) was obtained from Mr. B. Haeberle. A self fertile line from the cultivar 'Prolific' and the rye line 'Snoopy' which were available at the Plant Science Department were included. The lines of rye from Dr. Evans were from a collection from various origins and thus were genetically diverse. The selections from the material made available by Dr. Evans were based upon a visual assessment of S3 grain sample size, range of grain size between samples, and pigmentation. The visually selected rye lines are listed in Table 1. In order to further reduce the lines to a manageable number, an additional selection was based upon a protein analysis, and a twenty-five seed sample weight from each line. The lines were placed in three groups (small, medium, and large) based upon the seed weight. The protein content (nitrogen X 5.7 at 0.0% moisture) was determined by the Kjeldahl procedure on a small sample of S3 grain. The final selections indicated in Table 1 were made so that each weight group contained one purple pigmented line and the maximum range in protein possible.

The wheat used to produce primary triticales were the

TABLE 1. Identification and seed characteristics of rye lines (S.cereale), chosen for study.

Accession Number 2/	Field Number	Weight of 25 Seeds	Weight Class	Protein 1/	Pericarp Colour
2D30-4	23-4	0.850	large	16.4	non-purple
2D100-4	28-10	0.700	medium	17.8	non-purple
Mario Junrez-3	95-7	0.650	medium	23.7	non-purple
SFS SL purple-1	*100-1	0.500	small	21.9	purple
SFS SL purple-2	*106-3	0.600	medium	17.8	purple
SFS SL purple-3	112-6	0.550	medium	20.6	light purple
2D117-1	194-1	0.875	large	17.2	non-purple
2D117-1	*194-3	0.850	large	20.2	purple
2D2-4	*195-4	0.750	medium	18.6	non-purple
2D13-2	199-1	0.750	medium	18.6	non-purple
2D13-2	*199-3	0.700	medium	18.4	non-purple
2D14-5	209-4	0.750	medium	22.1	non-purple
2D82-7	*213-4	0.325	small	20.6	non-purple
2D14-2	204-1	0.275	small	23.5	non-purple
2D31-4	243-2	0.800	large	19.0	non-purple
2D29-2	*220-1	0.950	large	17.7	non-purple
2D31-3	*241-1	0.400	small	26.6	non-purple
2D83-3	*277-1	1.000	large	19.7	non-purple
2D31	320-2	0.600	medium	19.9	non-purple
CI 323387	*344-4	0.775	large	21.7	non-purple
2D4	349-1	0.575	medium	21.4	non-purple
SFP-5	*385-4	0.500	small	18.4	non-purple
2D82-3	*2D82-S5	0.575	medium	19.5	non-purple
2D82 self fertile	*2D82	0.650	medium	17.2	non-purple
----	*'Snoopy'	0.425	small	16.0	non-purple

* Lines selected for this study

1/ 0.0% moisture and Nitrogen X 5.7

2/ University of Manitoba accession number

semi-dwarf cultivars 'Sonora 64' (hexaploid) and 'Jori' (tetraploid). 'Sonora 64' originated from a breeding program at Centro Internacional de Mejoramiento de Maize y Trigo (CIMMYT) and 'Jori' also a CIMMYT introduction was obtained from Dr. D. Leisle of the Agriculture Canada Research Station located in Winnipeg. Plants from the commercial rye cultivar 'Prolific' grown from seed available at the Plant Science Department were used to produce the top-cross lines used in this study.

Production of Experimental Material

Triticale amphidiploids hybrids were synthesized using the wheat parent as the female and following the traditional method of emasculation and pollination. The wheat florets were clipped and the anthers removed with forceps. The spikes were then covered with glycine crossing bags until excision of the embryos occurred. Pollen was collected from the rye parent by bagging the spike before anthesis. A mixture of pollen from all rye plants in each line which flowered each day was dusted on the wheat stigmas. Crossing done in the greenhouse using this technique promoted embryo development without noticeable loss due to dessication of the embryo. Eighteen days after pollination, crossed spikes were removed, embryos were dissected out using sterile techniques, and were placed on nutrient agar medium in glass vials. After the plants were well established on the agar they were removed and transplanted in soil in three-inch clay pots. Glass vials were inverted over the seedlings for two days to prevent excessive

water loss until the plants had become established in the soil.

The hybrids were maintained in a growth cabinet at an 18 hour photoperiod and a day/night temperature of 18°C and 10°C, respectively. Root-tips were collected 2-3 weeks later after which the plants were repotted in five-inch clay pots and moved to the greenhouse. A root-tip chromosome count was conducted on each plant to verify its hybrid condition.

Hybrid plants were allowed to reach the 4-6 tiller stage before any attempt was made to double their chromosome number. A solution of either 0.1% colchicine or 0.1% colchicine plus 2.0% dimethyl sulfoxide was used to induce doubling. These concentrations were the same as those used by Subrahmanyam and Kasha (1975) and the Department of Plant Science, University of Manitoba. One vial containing either solution was inverted over the cut end of the primary tiller according to the capping method outlined by Bell (1950). Absorbent cotton was placed at the base of each plant to collect spillage from the vials. This precaution was found necessary to prevent injury to the roots of the treated plants while the vials were kept filled for 48 hours. The actual doubling period extended over two months but the treatment procedure was kept constant. Treated plants were allowed to mature in the greenhouse.

Of the original 14 rye lines used in the initial stages of this study, several were discarded because of their poor combining characteristics. The wheat-rye hybrid embryos from both 'Sonora 64' and 'Jori' crossed with inbred rye 241, 385, and 344 all failed to produce amphidiploids. The triticales

lines from the self fertile 2D82 line were very weak and did not produce C2 seed. The use of these four rye lines was discontinued at this point.

The wheat-rye hybrid embryos from 'Sonora 64' crossed with inbred 100 and inbred 106 as well as from 'Jori' crossed with inbred 199 failed to produce amphidiploids. The amphidiploids produced from the crosses 'Jori' by inbreds 2D82-S5 and 195 and from the crosses 'Sonora 64' by inbreds 195 and 213 could not be increased to the C3 generation. The hybrids from these wheat-rye crosses were lost but the parental ryes continued into this study.

The initial wheat-rye crosses were made in the greenhouse in January and February 1974. Chromosome doubling was conducted in the spring of 1974 in the greenhouse. The C2 seed harvested from the doubled plants was increased in the greenhouse during the fall and winter of 1974 to produce C3 seed. The C3 seed was used in the two experiments in which triticales was involved.

The original S3 rye lines were grown in the greenhouse where they were used as the pollen source for all of the crosses onto wheat and 'Prolific'. Self pollinated inbred seed was harvested from each of these plants. Based upon the quantity of grain, eight plants from each S3 inbred line were selected for comparison with the triticales and top-cross rye in the experiments. Whenever an experiment was conducted requiring inbred rye seeds a composite sample of S4 seed was used from these eight plants.

The general combining ability of a line in a cross pollinating species is an important character in determining the value of the line for hybrid production. The out-crossed variety 'Prolific' was used as the tester parent in top-crosses with each inbred line of rye which produced triticales. The top-cross, which is one of the several accepted means of determining general combining ability, was used in such a way that the inbred line of rye was the male parent and 'Prolific' was the female tester parent. This method of progeny testing of the inbred lines was used because it more closely approximates the synthesis of primary triticales than using the inbred lines as the maternal parent. Each inbred line was crossed onto at least 20 different individuals of 'Prolific' to reduce the variability present in the cross pollinated variety. A composite sample of pollen was collected and applied to the stigmas of 'Prolific' in the same manner as was done for the triticales production. A composite sample of equal quantities of seed from each of these 20 crosses was used for the progeny tests.

Experiments and Analyses

The plants were grown in four experiments. The plants in two of the experiments were identical inbred and top-cross rye material and were grown in the field and growth cabinet. Hexaploid or octoploid triticales lines in the remaining two experiments were grown in the growth cabinet. The limited quantity of triticales grain in each line prevented triticales

experiments from being conducted in the field.

The rye line 'Snoopy' was not grown in either rye experiment because it was not inbred and was not used to produce top-cross rye. 'Snoopy' was grown, along with one inbred and one top-cross line of rye, in a growth cabinet. It was necessary to obtain information about 'Snoopy' because it had been used as a parental rye line and therefore must be included among any comparisons between parental rye lines and their triticales hybrids.

An analysis of variance was calculated on the data from each character measured in the experiments with rye and triticales. A factorial analysis of variance utilizing replicates and treatments as factors was used for the individual plant data of the rye experiments. Three one-way analyses of variance were used to investigate the triticales data. The first one-way analysis of variance utilized the individual plant data of the twenty-one hexaploid and twenty-seven octoploid triticales lines. The second one-way analysis of variance of the triticales data was based upon the mean of each triticales line with triticales families as the treatments within the analysis. The third one-way analysis of variance utilizing individual plant data was conducted on the triticales lines (family) at each ploidy level from each inbred line. A triticales family was considered to be those lines of triticales originating from a common set of wheat and rye parents.

Correlation coefficients were calculated for the inbred and top-cross rye lines between the different environmental

conditions. Correlations for both inbred and top-cross rye lines between replicates 1 and 2 of the growth cabinet experiment were correlations between similar growth conditions. These correlations were based upon the mean of each line in each replicate. Thus the values used for the correlations were each a mean of 15 measurements. A second set of correlations for both inbred and top-cross rye lines between the rye experiments in the field and the growth cabinet were between different growth conditions. These correlations were based upon the mean of each inbred or top-cross rye line in the respective experiment. The means of the rye lines from the growth cabinet were based upon 30 measurements and the rye lines from the field were based upon a maximum of 64 measurements.

Correlation coefficients were calculated between the inbred and top-cross lines of rye for each character in each of the two experiments (field and growth cabinet). The analysis was based upon the mean of the individual plant measurements within each line of rye for the respective experiments.

Correlation coefficients were calculated among each pair of characters measured for the inbred and top-cross ryes grown in each experiment as well as for the hexaploid and octoploid triticales. The analyses utilized the mean of the individual plant measurements of each rye or triticales line in each experiment.

Plant Characteristics Measured

The following characters were used to assess the plant material studied in each experiment:

1. The number of days to heading.
2. Plant height (cm).
3. Length of the flag leaf (cm).
4. The number of spikes per plant.
5. Length of the first spike (cm) to emerge above the flag leaf.
6. The number of florets on the first spike to emerge above the flag leaf.
7. The number of florets per cm as calculated from the measurement of spike length and the number of florets per spike. This is a criterion of spike density.
8. The number of kernels per spike of the first spike to emerge above the flag leaf.
9. Fertility as calculated from the number of kernels per spike divided by the number of florets per spike.
10. Grain per plant (gm).
11. Dry weight per plant as the weight in grams after oven drying the above-ground portion of each plant.
12. Harvest index as calculated from the weight of grain per plant divided by the dry weight per plant.
13. Kernel weight as the weight of two hundred seeds (gm).
14. Straw and grain protein as a Kjeldahl nitrogen determination multiplied by 5.7 on a 0.0% moisture basis from composite samples.



Growth Conditions

The rye experiment grown in the field (inbred and top-cross rye lines) contained eight replicates with eight measured plants in each row. The rows were 30 cms. apart with 15 cms. between plants within the rows. Each replicate contained one row of each inbred and top-cross line. The experimental rows were alternated with the rye cultivar 'Gazelle' to provide a uniform set of environmental conditions within this experiment. The measurements of the standing plants were taken about one week before harvesting.

Plants of the second rye experiment plus the triticales experiments were each grown under identical plant arrangements and growth conditions in a growth cabinet. The seeds were germinated in plastic boxes and transplanted to the growth cabinet at the 1-2 leaf stage. Three plants were assigned randomly to each of the six-inch clay pots except that not more than one plant from each line was planted in each pot. Fertilization and other cultural practices were kept uniform between experiments.

The second rye experiment contained fifteen plants of each of the nine inbred and top-cross rye lines. The plants were grown in a growth cabinet (replicate 1) and then repeated in the same growth cabinet (replicate 2) to give a total of 30 plants in 2 replicates. The plants were removed from the growth cabinet after 72 days for replicate 1 and 73 days for replicate 2.

The triticales experiments contained 21 hexaploid

triticale lines in one cabinet and 27 octoploid triticale lines in a second growth cabinet. The 21 lines of hexaploid triticale, derived from seven rye lines, were each represented in the experiment by 14 plants. The 27 lines of octoploid triticale, derived from five rye lines, were each represented by 10 plants. The plant of both experiments were removed from the growth cabinet after 74 days.

The growth cabinet was maintained under identical control settings for each of the three experiments and was operated in a manner to simulate natural growing conditions. A night temperature of 15°C was increased hourly for 6 hours until reaching 20°C which was maintained for 6 hours. At night the temperature was lowered in an identical stepwise fashion followed by 6 hours at 15°C. After 6 hours of darkness at 15°C, lights were automatically returned to full illumination (2200 foot candles) in three stages. Similarly, after 14 hours photoperiod, illumination was reduced to zero through the same three stages.

The plants were removed from the growth cabinets when they had headed and the grain of the earliest spikes was beginning to ripen. Just prior to their removal from the cabinet the following measurements were taken; plant height, flag leaf length, number of spikes per plant, spike length, and number of florets per spike. The plants were placed in the greenhouse where watering was continued for two to three weeks before drying and harvesting.

The spikes and straw were harvested separately and oven-dried for two days at 40°C. Dry weights and kernel number per

spike were recorded after which the material was threshed and grain weight per plant was taken. Plant and grain samples were analysed for nitrogen content using the Kjeldahl technique. Samples used for kernel weight, straw and grain protein were composites from several plants within each treatment. The same plants were used to contribute the sample for each of the three measurements taken from composite material.

RESULTS

The results have been arranged in four major sections. The first section contains the information acquired from synthesis of hexaploid and octoploid triticales. The second section contains the information obtained from grass dwarfing, pericarp colour, and 'Snoopy' rye. The third section contains all of the calculations performed on the rye data. The fourth section contains information acquired from the experiments with hexaploid and octoploid triticales.

Synthesis Techniques

The hexaploid triticales was produced from the tetraploid wheat cultivar 'Jori'. Only a few spikes of each wheat-rye cross were necessary because of the excellent degree of successful pollination (Table 2). By the tenth day after pollination the developing seeds appeared large and healthy and had apparently reached their maximum development in vivo by that time. An average of 11.8 embryos per spike were excised. These embryos were all very poorly developed and usually appeared as a round mass of cells. The eighteen-day old seed quite often contained a watery solution giving the seed a healthy appearance even though the embryo and endosperm had not developed to a stage comparable to that of normal wheat or the wheat-rye embryos from 'Sonora 64'. Only a few of the embryos developed into seedlings with 6% producing mature plants and 2% producing

TABLE 2. Results of crosses between tetraploid wheat cultivar, 'Jori', and fourteen rye lines.

Rye Line	Spikes Crossed	Embryos Cultured	Triticale Hybrids		Amphidiploids	
			Number	As Percentage of Embryos	Number	As Percentage of Embryos
199	6	62	2	3	0	0
213	9	137	5	4	4	80
277	2	18	6	33	1	17
194	8	114	5	4	3	60
2D82-S5	6	82	5	6	1	20
100	8	90	11	12	2	18
106	7	95	5	5	2	40
195	6	96	10	10	2	20
220	6	99	6	6	4	67
'Snoopy'	3	40	8	20	5	63
241	6	65	1	2	0	0
385	8	94	0	0	0	0
344	15	75	6	8	0	0
2D82 Self fertile	5	61	3	5	1	33
Total	95	1128	73		25	

TABLE 3. Results of crosses between hexaploid wheat cultivar, 'Sonora 64', and fourteen rye lines.

Rye Line	Spikes Crossed	Embryos Cultured	Triticale Hybrids		Amphidiploids	
			Number	As Percentage of Embryos	Number	As Percentage of Hybrids
199	9	94	38(25) ¹	40	10	26
213	4	22	11	50	2	18
277	9	82	64	78	3	5
194	12	43	18	42	5	28
2D82-S5	19	90	66	73	11	17
100	11	10	7	70	0	0
106	11	39	12	31	0	0
195	15	32	29	91	1	3
220	14	16	11	69	4	36
'Snoopy'	10	25	19	76	8	42
241	5	11	6	55	0	0
385	18	134	0(82)	0	0	0
344	10	37	2	5	0	0
2D82 self fertile	4	18	16(9)	89	1	6
Total	151	653	299		45	

1/ figures in parenthesis indicate grass dwarf mutants obtained in addition to the normal plants.

amphidiploids.

A larger number of spikes from the hexaploid wheat cultivar 'Sonora 64' was crossed in comparison to the number of crossed spikes on the cultivar 'Jori' because of the lower number of embryos produced (average 4.3 per spike). All embryos were large and well developed and consequently their rate of germination on the agar was high. Forty-six percent of the embryos cultured reach maturity but only 7% produced amphidiploids (Table 3).

A 0.1% solution of colchicine applied independently of the surfactant doubled the chromosome number in 9 of 31 plants (29%) of the 'Jori' X rye crosses, while colchicine + dimethyl sulfoxide doubled the chromosome number in 6 of 23 plants (26%) (Table 4). In the cross 'Sonora 64' X rye, colchicine alone doubled 19 of 136 plants (14%) while colchicine + dimethyl sulfoxide doubled 17 of 126 plants (13%). The addition of 2.0% dimethyl sulfoxide to 0.1% colchicine was no more effective than 0.1% colchicine alone in producing amphidiploids in either cross using the technique employed in this study.

Grass Dwarfing, Pericarp Colour, and 'Snoopy' Rye

1. Grass Dwarfing

Grass dwarfs were observed in the progeny of three crosses involving 'Sonora 64' (Table 3). The hybrid embryos which were grass dwarf germinated normally in vitro. At the 2- to 3-leaf stage, the seedlings began to exhibit grass dwarf characteristics. Growth became very slow and only a small

TABLE 4. Comparison of aqueous colchicine solution versus aqueous colchicine solution plus surfactant (dimethyl sulfoxide) on the doubling frequency of tetraploid and hexaploid wheat-rye hybrids.

Cross	0.1 colchicine		
	Plants Treated	Plants Doubled	Percentage Doubled
'Jori' X diploid rye lines	31	9	29%
'Sonora 64' X diploid rye lines	136	19	14%
Cross	0.1% colchicine + 2.0% dimethyl sulfoxide		
	Plants Treated	Plants Doubled	Percentage Doubled
'Jori' X diploid rye lines	23	6	26%
'Sonora 64' X diploid rye lines	126	17	13%

rosette of leaves was produced regardless of whether the plant was left on the agar or transplanted to soil. None of the grass dwarfs produced grain although several plants of the cross of 'Sonora 64' with the self-fertile 2D82 received an application of colchicine and reached maturity. No evidence of grass dwarfing among hexaploid triticales or inbred and top-cross ryes was obtained. A Chi Square test indicated that the ratios of normal and dwarf hybrids from the crosses 'Sonora 64' by 2D82 self-fertile and inbred 199 could fit a 1:1 ratio.

2. Pericarp Colour

Three lines of inbred rye which possessed a purple seed colour (lines 194, 100, and 106) were used throughout the study. Visual examination showed that the purple colouring was confined to the pericarp. There was some variation in the intensity of the purple colour in the rye lines but purple and non-purple phenotypes were readily distinguished. All of the lines lacking a purple pericarp remained 100% non-purple during inbreeding, top-crossing, and synthesis of triticales.

Inbred line 106 consistently produced seed through the S4 and out-crossed generations with a purple pericarp but inbred lines 194 and 100 produced non-purple segregates. All of the top-cross plants and hexaploid triticales produced using pollen from S3 plants of inbred 106 produced seed with a purple pericarp. The classification of the purple versus non-purple colour in rye experiments was based upon grain from

S4 plants (Table 5). In all of the cases where the grain was from inbred parents a ratio of 3 purple : 1 non-purple was found. In 3 of the 4 top-crossed populations, the results fit a 1:1 ratio (Table 5).

The three hexaploid triticales families synthesized from inbred rye with a purple pericarps contained coloured grain. The two hexaploid triticales families from each of the inbred rye lines, 100 and 106, produced uniformly coloured grain. The three hexaploid triticales lines within the family from inbred rye 194 exhibited variation in the colour intensity. The colour intensity varied within and between the three hexaploid triticales lines. There was no suggestion of a definite inheritance pattern within hexaploid triticales from inbred rye line 194.

The only octoploid triticales produced from a purple pericarp rye were from inbred 194. All five of these triticales lines failed to exhibit purple pericarp.

3. 'Snoopy' Rye

Since the rye line 'Snoopy' was not inbred and therefore was not used to produce top-cross rye, it was excluded from the rye experiments in the growth cabinet and in the field. However, it was utilized to produce amphidiploids at the hexaploid and octoploid levels. Plants from the rye line 'Snoopy' were grown in a growth cabinet to generate data for comparisons among parental rye lines. Plants from inbred line 2D82-S5 and top-cross line 194 were grown with 'Snoopy'

TABLE 5. Segregation pattern of pericarp colour in inbred rye lines 194 and 100 in the growth cabinet and field experiments.

	Purple	Non-purple	Ratio	χ^2	P
Inbred Rye 194					
Growth Cabinet	23	7	3:1	0.04	0.90-0.75
Field	48	15	3:1	0.04	0.90-0.75
Inbred Rye 100					
Growth Cabinet	23	5	3:1	0.76	0.50-0.25
Field	48	10	3:1	1.86	0.25-0.10
Top-Cross Rye 194					
Growth Cabinet	16	13	1:1	0.31	0.75-0.50
Field	40	24	1:1	4.00	0.05-0.025
Top Cross Rye 100					
Growth Cabinet	14	16	1:1	0.13	0.75-0.50
Field	29	35	1:1	0.56	0.50-0.25

to determine if the 'Snoopy' data could be included with the inbred rye data from the growth cabinet experiment. The number of observations and means of each of the fifteen characters from these three lines of rye are presented in Appendix V. At least half of the character means for inbred 2D82-S5 and top-cross 194 listed in Appendix V fall between the corresponding means in replicates 1 and 2 in the growth cabinet experiment with rye (Appendix II). Therefore, the means of the fifteen plant characteristics from 'Snoopy' rye were included with the means from the other parental rye lines grown in the growth cabinet. These combined data were used to determine the correlation coefficients among the plant characteristics reported later in this study.

Interrelationships Among Rye Lines

1. Variance Components

Inbred and top-cross lines of rye were grown in two replicates in the growth cabinet and in eight replicates in the field. Individual plant measurements were taken for each plant in the growth cabinet and on eight plants from each treatment in the field. Approximately half of the characters of inbred and top-cross rye shifted in their values between the growth cabinet and field experiments (Appendices I and II). The number of spikes per plant, fertility, grain per plant, and dry weight per plant were the characters most drastically affected by moving from the growth cabinet to the field environment. Factorial analyses of variance were performed

using individual plant data for each character to give a measure of the genetic variability among the inbred and top-cross lines (Tables 6 to 9 inclusive). The number of observations and the mean of each treatment for the rye experiments are presented in Appendices I and II.

The results of the factorial analyses of variance indicated that there was a significant difference among the inbred lines of rye in the growth cabinet and in the field for each of the characters (Tables 6 and 8). Top-cross rye in the growth cabinet experiment did not contain any lines which were significantly different from the rest of the lines for the character of plant height (Table 7). The results from all of the other analyses of variance using individual plant data from top-cross lines of rye indicated significant differences among the lines of rye (Tables 7 and 9).

The results of the factorial analyses of variance for the replications in the rye experiments (Tables 6 to 9 inclusive) indicated a significant difference between replicates for approximately half of the characters. Two aspects were considered when conducting replicate analyses, (1) uniformity in the significant and non-significant replicate F-test values within each of the inbred and top-cross rye lines in the two environments, and (2) uniformity within each of the field and growth cabinet environments for the rye lines.

Observations concerning the first aspect illustrated that the majority of the inbred rye characteristics contained significantly different replicates for each character in only

TABLE 6. Mean square values and significance from the analysis of variance of fifteen plant characteristics for the inbred rye lines in the growth cabinet experiment.

Character	Cabinet	Line	Interaction	Error
1 Days to Heading	102.74	771.68**	20.51	29.55
2 Plant Height	1736.60*	759.89*	768.04*	334.41
3 Flag Leaf Length	105.40**	82.70**	20.83**	7.25
4 Spike Number	41.50**	37.59**	5.49	3.95
5 Spike Length	9.32**	26.27**	3.01	1.35
6 Florets/Spike	646.98**	1551.36**	88.26	75.20
7 Florets/cm	0.94	7.17**	0.96	0.71
8 Kernels/Spike	1499.70**	1320.47**	160.25	98.10
9 Fertility	0.36**	0.41**	0.03	0.03
10 Grain/Plant	7.39**	3.77**	1.10	0.64
11 Dry Weight/Plant	40.48**	35.58**	7.73	4.75
12 Harvest Index	0.03	0.13**	0.01	0.01
13 Kernel Weight	14.73**	2.81**	0.44	0.22
14 Straw Protein	2.80	9.51**	1.53	0.72
15 Grain Protein	28.93**	13.40**	2.98*	1.25

* significant at the 5% level

** significant at the 1% level

TABLE 7. Mean square values and significance from the analysis of variance of fifteen plant characteristics for the top cross rye lines in the growth cabinet experiment.

Character	Cabinet	Line	Interaction	Error
1 Days to Heading	47.19	77.08**	7.18	25.92
2 Plant Height	2912.15**	122.24	313.70	186.74
3 Flag Leaf Length	97.16**	26.21**	20.51*	10.12
4 Spike Number	420.66**	19.50**	2.50	5.32
5 Spike Length	2.35	3.72*	1.04	1.58
6 Florets/Spike	1492.93**	373.60**	123.71	78.49
7 Florets/cm	7.28**	1.78*	0.30	0.82
8 Kernels/Spike	1568.18**	661.49**	103.67	94.72
9 Fertility	0.08	0.18**	0.01	0.02
10 Grain/Plant	0.22	16.78**	2.56	3.25
11 Dry Weight/Plant	32.87	51.97**	15.67	16.18
12 Harvest Index	0.02*	0.03**	0.01	0.01
13 Kernel Weight	12.62**	1.45**	0.29	0.24
14 Straw Protein	23.34**	5.45**	1.42*	0.64
15 Grain Protein	1.93	3.36**	0.90	0.64

* significant at the 5% level

** significant at the 1% level

TABLE 8. Mean square values and significance from the analysis of variance of the twelve plant characteristics on which individual plant data were recorded for top-cross rye lines in the field experiment.

Character	Replicate	Line	Interaction	Error
1 Days to Heading	161.34**	404.79**	42.79*	23.56
2 Plant Height	1213.42**	7311.95**	275.37	226.09
3 Flag Leaf Length	8.86	91.02**	10.47	8.63
4 Spike Number	109.82**	287.02**	40.91**	21.15
5 Spike Length	2.95	38.90**	1.82	2.60
6 Florets/Spike	27.36	1778.48**	64.00	61.88
7 Florets/cm	0.94*	6.47**	0.38	0.45
8 Kernels/Spike	318.01	2939.73**	203.19	189.18
9 Fertility	0.11	0.87**	0.07	0.06
10 Grain/Plant	50.32**	68.90**	17.61	14.87
11 Dry Weight/Plant	537.32**	1358.35**	222.41	147.92
12 Harvest Index	0.02**	0.12**	0.01	0.01

* significant at the 5% level
 ** significant at the 1% level

TABLE 9. Mean square values and significance from the analysis of variance of the plant characteristics on which individual plant data were recorded for top-cross rye lines in the field experiment.

Character	Replicate	Line	Interaction	Error
1 Days to Heading	55.64**	79.95**	24.02**	9.29
2 Plant Height	312.07**	596.79**	152.36	106.57
3 Flag Leaf Length	21.82	52.89**	7.89	10.97
4 Spike Number	100.75**	113.75**	31.76	34.07
5 Spike Length	6.21**	7.93**	1.84	2.05
6 Florets/Spike	84.93	411.63**	38.44	49.12
7 Florets/cm	1.56**	1.92**	0.43**	0.33
8 Kernels/Spike	208.29	1971.38**	157.09	132.29
9 Fertility	0.03	0.54**	0.05	0.03
10 Grain/Plant	211.54**	302.90**	80.29	72.45
11 Dry Weight/Plant	1113.00*	1338.25**	414.02	479.42
12 Harvest Index	0.02**	0.03**	0.01	0.004

* significant at the 5% level

** significant at the 1% level

one of the experiments (field or growth cabinet, Tables 6 and 8). A similar situation existed for the top-cross rye lines (Tables 7 and 9). The lines of inbred and top-cross rye were significantly different in both experiments for plant height and spike number per plant. However, these were the only characters which expressed such uniformity in their sensitivity to the environment.

Observations concerning the second method illustrated that the presence of a significant or non-significant F-test for replicates was consistent for inbred and top-cross rye lines in the field experiment (Tables 8 and 9). Only spike length failed to produce a consistent replicate F-test result. Thus, in the field experiment both inbred and top-cross rye lines react in a similar fashion to the differences between replications. The genetical factors of the plant characteristics sensitive to slight environmental changes were present in both inbred and top-cross lines of rye. The results of these analyses of variance indicated that flag leaf length, florets per spike, kernels per spike, and fertility were not sensitive to the environmental differences between the replicates of the field experiment.

Observations concerning the second aspect did not illustrate the same uniformity of the replicate F-test values in the growth cabinet experiment as was the case in the field rye experiment. The inbred and top-cross rye lines in the growth cabinet experiment (Tables 6 and 7) did not contain any uniformity between the F-test values for inbred and

top-cross rye lines.

The interaction between replicates and lines of rye were significant for only a few characters (Tables 6 to 9 inclusive). The characters which contained significant interactions were not consistent between growth cabinet and field conditions or between inbred and top-cross rye.

The main points from these analyses of variance are:

(1) The results of the F-test revealed significant differences among the inbred and top-cross lines of rye for the characters measured. Thus, there was genetic variation among all of the characters in inbred and top-cross rye which would prove beneficial in selection for these characters. (2) The same characters of both inbred and top-cross rye were genetically sensitive to environmental differences between replications of the field experiment but not the growth cabinet experiment. (3) The response to the environmental differences between replicates was generally the same for all inbred and top-cross rye lines. This was indicated by the lack of a significant interaction between lines and replicates.

2. Correlation Between Environments

These correlations were calculated to determine if the inbred and top-cross rye lines maintained a consistent order, relative to one another, when grown in different environments. The results have been divided into two sets and the correlation coefficients are presented in Table 10. The first set shows the correlation for the inbred and top-cross rye lines

TABLE 10. Correlation coefficients between growth cabinets and between growth cabinet and field experiments for the inbred and top-cross rye lines.

	<u>Different Environments</u>		<u>Similar Environments</u>	
	1/	2/	3/	4/
1 Days to Heading	0.45	0.69*	0.99**	0.83**
2 Plant Height	0.42	0.49	-0.01	-0.44
3 Flag Leaf Length	0.74*	0.26	0.61	0.12
4 Spike Number	0.44	0.19	0.75*	0.80**
5 Spike Length	0.63	0.49	0.79*	0.58
6 Florets/Spike	0.80**	0.89**	0.89**	0.55
7 Florets/cm	0.76*	0.65	0.77*	0.28
8 Kernels/Spike	0.72*	0.87**	0.83**	0.74*
9 Fertility	0.72*	0.91**	0.88**	0.92**
10 Grain/Plant	0.50	0.62	0.76*	0.76*
11 Dry Weight/Plant	0.48	0.45	0.72*	0.55
12 Harvest Index	0.86**	0.74**	0.91**	0.73*
13 Kernel Weight	0.90**	0.83**	0.82**	0.74*
14 Straw Protein	0.25	0.91**	0.91**	0.69*
15 Grain Protein	0.50	0.34	0.64	0.59

1/ inbred rye of growth cabinet versus inbred rye of field

2/ top-cross rye of growth cabinet versus top-cross rye of field

3/ inbred rye of replicate 1 versus replicate 2 of growth cabinet

4/ top-cross rye of replicate 1 versus replicate 2 of growth cabinet

* significant at the 5% level

** significant at the 1% level

grown under different conditions (growth cabinet and field). The second set of correlations was between similar growth conditions (replicate 1 and 2 of the growth cabinet experiment).

The number of kernels per spike, fertility, harvest index and kernel weight were the characters for which both inbred and top-cross rye lines were correlated in similar and different growth conditions. The relative order of the rye lines for these characters was not altered by changing the environment. At the other extreme, the rye lines were not correlated for plant height or grain protein between any environments. Of the remaining 9 characters, three were correlated for 3 of the 4 comparisons (Table 10). Days to heading and straw protein were correlated under similar growth conditions. However, these two characters were not correlated for inbred rye lines under different growth conditions. The number of florets per spike was not correlated for top-cross rye lines in similar growth conditions. The remaining 7 characters were correlated for only 1 or 2 of the comparisons (Table 10).

These calculations illustrate the relative stability of the characters of inbred and top-cross lines of rye grown under different environmental conditions. The results can be used as an indication of the degree of control over growth conditions required for the individual character to insure consistent data between replicates and experiments.

3. Correlations Between Inbred and Top-Cross Rye

The relationship between inbred and top-cross rye for the individual characters was determined by correlation studies using the inbred and top-cross line means from the growth cabinet and field experiments. The data in Table 11 illustrate that a positive correlation existed between the inbred and top-cross lines of rye grown in the field for twelve of the fifteen characters. Days to heading, plant height, and florets per cm were not correlated between inbred and top-cross rye lines. Similar correlation coefficients from the growth cabinet were smaller and thus contained fewer significant comparisons (Table 11). However, the correlation coefficients between inbred and top-cross rye lines in the growth cabinet experiment were of the same relative size as those in the field experiment. Therefore, the phenotypic expression of the majority of characters among inbred lines of rye was expressed among top-cross lines of rye.

4. Correlations Among Characters of Inbred Rye

The correlations calculated among the fifteen characters measured on the lines of inbred rye grown in the growth cabinet and in the field were based upon the means from each inbred line of rye (Appendices I and II). The correlation coefficients from these calculations on inbred rye are presented in Tables 12 and 13.

The significant negative correlation coefficients among the characters measured on the lines of inbred rye involved

TABLE 11. Correlation coefficients between inbred and top-cross rye lines grown in the growth cabinet and field experiments.

Character	Growth Cabinet	Field
1 Days to Heading	0.01	0.30
2 Plant Height	0.18	0.29
3 Flag Leaf Length	0.57	0.80**
4 Spike Number	0.67*	0.75*
5 Spike Length	0.66	0.81**
6 Florets/Spike	0.70*	0.93**
7 Florets/cm	0.54	0.65
8 Kernels/Spike	0.86**	0.84**
9 Fertility	0.76*	0.78*
10 Grain/Plant	0.74*	0.74*
11 Dry Weight/Plant	0.58	0.72*
12 Harvest Index	0.70*	0.71*
13 Kernel/Weight	0.62	0.77*
14 Straw Protein	0.81**	0.70*
15 Grain Protein	0.49	0.78*

* significant at the 5% level

** significant at the 1% level

TABLE 12. Simple phenotypic correlation coefficients between pairs of characters for nine parental rye lines grown in the field.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Days to Heading														
2 Plant Height	-0.20													
3 Flag Leaf Length	-0.17	0.00												
4 Spike Number	-0.35	0.84**	-0.31											
5 Spike Length	0.51	0.09	0.30	-0.08										
6 Florets/Spike	0.28	0.20	0.19	0.00	0.84**									
7 Florets/cm	-0.21	0.27	-0.05	0.12	0.10	0.61								
8 Kernels/Spike	0.05	0.27	0.58	-0.22	0.39	0.57	0.53							
9 Fertility	0.01	0.14	0.37	-0.26	0.17	0.48	0.65	0.87**						
10 Grain/Plant	-0.10	0.90**	0.03	0.73*	0.26	0.22	0.06	0.32	0.10					
11 Dry Weight/Plant	-0.02	0.93**	-0.20	0.89**	0.22	0.21	0.09	0.06	-0.05	0.91**				
12 Harvest Index	-0.14	-0.17	0.64	-0.51	0.16	0.11	0.01	0.72*	0.56	0.08	-0.31			
13 Kernel Weight	0.14	0.29	-0.06	0.24	0.17	-0.21	-0.56	-0.13	-0.29	0.58	0.45	0.17		
14 Straw Protein	0.44	-0.28	0.10	-0.34	0.76*	0.82**	0.37	0.24	0.33	-0.27	-0.18	-0.02	-0.30	
15 Grain Protein	0.21	0.56	-0.40	0.50	-0.32	-0.23	0.08	0.00	0.12	0.43	0.58	-0.36	0.07	-0.41

* significant at the 5% level

** significant at the 1% level

TABLE 13. Simple phenotypic correlation coefficients between pairs of characters for ten parental rye lines grown in the growth cabinet.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Days to Heading														
2 Plant Height	-0.37													
3 Flag Leaf Length	-0.52	0.43												
4 Spike Number	-0.37	0.80**	0.11											
5 Spike Length	-0.72	0.27	0.71*	0.20										
6 Florets/Spike	-0.52	0.27	0.43	0.27	0.83**									
7 Florets/cm	0.06	0.13	-0.25	0.22	0.50	0.59								
8 Kernels/Spike	-0.74	0.57	0.66*	0.31	0.83**	0.64*	-0.02							
9 Fertility	-0.76*	0.54	0.62	0.29	0.70*	0.36	-0.33	0.94**						
10 Grain/Plant	-0.40	0.74*	0.41	0.74*	0.52	0.41	-0.02	0.60	0.58					
11 Dry Weight/Plant	-0.24	0.75*	0.28	0.86**	0.38	0.44	0.24	0.39	0.30	0.93**				
12 Harvest Index	-0.74*	0.52	0.41	0.43	0.59	0.26	-0.35	0.82**	0.92**	0.71	0.44			
13 Kernel Weight	0.05	0.00	0.00	0.28	0.07	-0.03	-0.16	-0.14	-0.11	0.56	0.55	0.18		
14 Straw Protein	0.59	-0.24	-0.36	-0.08	-0.25	0.17	0.60	-0.54	-0.74*	-0.22	0.05	-0.72*	0.10	
15 Grain Protein	0.40	0.03	0.12	-0.09	-0.43	-0.49	-0.27	-0.47	-0.35	-0.19	-0.06	-0.43	0.03	0.06

* significant at the 5% level

** significant at the 1% level

days to heading, and straw protein and all occurred in the growth cabinet experiment. Days to heading was negative correlated with spike length and kernels per spike. Both days to heading and straw protein were negatively correlated with the characters measuring the efficiency of spike and plant grain production (fertility and harvest index). The results from inbred rye in the field showed a positive correlation between straw protein and the spike characters of spike length and florets per spike.

Plant height was positively correlated with spike number, grain per plant and dry weight per plant among the inbred lines in the growth cabinet and in the field experiments.

Flag leaf length was positively correlated with spike length and kernels per spike among the inbred lines of rye in the growth cabinet. The field trial did not contain any significant correlations with flag leaf length.

The number of spikes per plant was positively correlated with grain per plant and dry weight per plant in both experiments with inbred rye.

The correlation coefficients in the growth cabinet showed that spike length was positively correlated with florets per spike, kernels per spike, and fertility. The results of the field experiment showed a positive correlation between spike length and florets per spike as well as the previously mentioned correlation with straw protein.

The number of kernels per spike, fertility, and harvest index were positively intercorrelated for the inbred

lines of rye grown in the growth cabinet. The field experiment of inbred rye contained positive correlations between kernels per spike and the characters fertility and harvest index. Grain per plant was positively correlated with dry weight per plant in both inbred rye experiments. The correlation between grain yield per plant and harvest index was significantly positive only in the growth cabinet experiment.

The small number of parental lines of rye meant a high correlation coefficient had to be obtained to indicate significance (field experiment $r=0.67$, growth cabinet $r=0.63$). These high values allowed only a few comparisons to be designated as significantly correlated. The strength of the correlations was greatly increased by the large number of observations in each of the means used to calculate the correlation coefficient (field experiment maximum of 64 and growth cabinet maximum of 30). The correlations were also strengthened by the similarity in the results between the two experiments with inbred rye.

5. Correlations Among Characters of Top-Cross Rye

The correlations calculated among the fifteen characters measured for the top-cross lines of rye were conducted in the same manner as those on the inbred lines of rye. The correlation coefficients for this experiment were based upon the overall mean of each top-cross rye line from the growth cabinet and field experiments (Tables 14 and 15).

The significant negative correlation coefficients among

TABLE 14. Simple phenotypic correlation coefficients between pairs of characters for nine top-cross rye lines grown in the field.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Days to Heading														
2 Plant Height	-0.62													
3 Flag Leaf Length	0.08	0.08												
4 Spike Number	-0.80**	0.68*	-0.33											
5 Spike Length	0.42	0.03	0.45	0.48										
6 Florets/Spike	-0.19	0.43	-0.04	0.07	0.64									
7 Florets/cm	-0.68*	0.54	-0.48	0.62	-0.15	0.65								
8 Kernels/Spike	-0.04	-0.08	0.09	-0.11	0.18	0.33	0.32							
9 Fertility	0.04	-0.23	0.17	-0.17	-0.01	0.00	0.09	0.94**						
10 Grain/Plant	-0.40	0.70*	0.13	0.56	0.06	0.34	0.47	0.51	0.41					
11 Dry Weight/Plant	-0.56	0.87**	0.19	0.70*	0.06	0.34	0.45	0.18	0.06	0.92**				
12 Harvest Index	-0.10	0.32	0.10	0.27	0.10	0.27	0.35	0.77*	0.72*	0.88**	0.63			
13 Kernel Weight	-0.12	0.62	0.19	0.42	0.04	-0.05	-0.11	-0.60	-0.62	0.33	0.60	-0.02		
14 Straw Protein	0.10	-0.37	-0.07	-0.39	0.29	0.37	0.10	-0.23	-0.35	-0.68*	-0.59	-0.58	-0.34	
15 Grain Protein	-0.17	0.40	0.19	0.06	0.19	-0.27	-0.23	-0.37	-0.32	0.06	0.24	-0.27	0.47	-0.39

* significant at the 5% level

** significant at the 1% level

TABLE 15. Simple phenotypic correlation coefficients between pairs of characters for nine top-cross rye lines grown in the growth cabinet.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Days to Heading														
2 Plant Height	-0.30													
3 Flag Leaf Length	-0.21	0.05												
4 Spike Number	-0.59	0.16	-0.42											
5 Spike Length	-0.47	-0.29	0.53	-0.17										
6 Florets/Spike	-0.03	-0.12	0.57	-0.34	0.63									
7 Florets/cm	0.12	0.03	0.47	-0.41	0.42	0.80**								
8 Kernels/Spike	-0.48	-0.14	0.04	0.41	0.61	0.20	-0.02							
9 Fertility	-0.43	-0.11	-0.22	0.54	0.31	-0.27	-0.40	0.89**						
10 Grain/Plant	-0.57	-0.02	-0.23	0.87**	0.09	-0.30	-0.35	0.61	0.75*					
11 Dry Weight/Plant	-0.53	-0.02	-0.26	0.85**	0.10	-0.16	-0.22	0.55	0.62	0.96**				
12 Harvest Index	-0.50	0.03	-0.19	0.71*	0.04	-0.48	-0.51	0.70*	0.90**	0.83**	0.66			
13 Kernel Weight	-0.04	0.29	-0.02	0.03	-0.41	-0.47	-0.08	-0.66	-0.43	0.03	0.04	-0.15		
14 Straw Protein	0.43	-0.19	0.02	-0.42	-0.08	0.54	0.36	-0.49	-0.73*	-0.70*	-0.54	-0.84**	-0.22	
15 Grain Protein	0.64	0.09	0.11	-0.35	-0.50	0.14	0.34	-0.70*	-0.73*	-0.37	-0.23	-0.61	0.44	0.41

* significant at the 5% level

** significant at the 1% level

the characters of top-cross rye were with days to heading and straw protein in the field experiment. Days to heading was negatively correlated with spike number and florets per cm among the top-cross lines of rye grown in the field. Straw protein was negatively correlated with grain per plant in the field experiment. The growth cabinet experiment contained negative correlation coefficients with straw protein and grain protein. Straw protein was also negatively correlated with fertility, grain per plant, and harvest index in the growth cabinet. Grain protein was negatively correlated with kernels per spike and fertility among the top-cross rye lines in the growth cabinet but not in the field.

Plant height was positively correlated with spike number, grain per plant, and dry weight per plant in the field experiment. Plant height of the top-cross rye lines was not correlated with any of the characters in the growth cabinet.

The number of spikes per plant was positively correlated with harvest index, grain per plant, and dry weight per plant among the top-cross rye lines grown in the growth cabinet. The positive correlation between spike number and dry weight per plant also existed in the field experiment. The number of florets per spike was positively correlated with the number of florets per cm among the top-cross lines of rye in the growth cabinet experiment.

The number of kernels per spike, fertility, grain per plant, and harvest index were generally intercorrelated among the top-cross lines of rye grown under growth cabinet conditions.

The only exception to the intercorrelations was the lack of a significant correlation between kernels per spike and grain per plant. Four positive correlations existed among these four characters of the top-cross lines of rye grown in the field. The number of kernels per spike, fertility, and harvest index were intercorrelated. Grain yield per plant was correlated with harvest index in the field experiment. Grain yield per plant was also positively correlated with dry weight per plant in both experiments.

The high correlation coefficient ($r=0.67$) required to indicate significance dictated that only a few comparisons were significantly correlated. These correlations were strengthened by the large number of observations in each mean used for the calculations (field experiment a maximum of 64 and growth cabinet a maximum of 30) and the similarity between the field and growth cabinet results.

Interrelationship Among Triticale Lines

1. Variance Components

The results from the three sets of analyses of variance on hexaploid and octoploid triticales lines determined the existence of genetic variation and its probable source. The number of observations and the means of each treatment for hexaploid triticales and octoploid triticales which were used in the analyses of variance are presented in Appendices III and IV.

The first one-way analyses of variance was calculated for individual characters of the twenty-one hexaploid and twenty-seven octoploid triticales lines (Table 16). These analyses of variance were based upon individual plant observations. The results of the F-test for all characters at both ploidy levels indicated significant differences among the lines of triticales.

A second one-way analyses of variance was performed between the triticales families at each ploidy level using the means from each of the twenty-one and twenty-seven triticales lines (Table 17). The triticales families at each ploidy level originated from a different rye line. All of the characters except grain protein contained significant differences among the seven hexaploid triticales families. By contrast, the results of the octoploid triticales indicated significant differences among the five octoploid triticales families for the characters days to heading, plant height, and spike length.

The third one-way analyses of variance performed for the characters was based upon individual plant observations. However, the treatments were composed of the triticales lines within each family at each ploidy level (Tables 18 and 19). The results of these analyses of variance illustrate the variation among the triticales lines originating from each rye line. The hexaploid triticales families from the rye lines, 'Snoopy', inbred 220, and inbred 194, contained significantly different lines for many of the characters measured (Table 18). The hexaploid triticales lines within the three remaining

TABLE 16. Mean square values and significance from the analysis of variance of the plant characteristics for the hexaploid and octoploid triticale lines.

Character	Hexaploid Triticale	Error	Octoploid Triticale	Error
1 Days to Heading	456.08**	8.02	117.34**	11.58
2 Plant Height	1469.24**	167.41	719.56**	86.32
3 Flag Leaf Length	59.48**	21.73	38.10**	13.87
4 Spike Number	24.81**	1.44	11.08**	2.78
5 Spike Length	29.92**	1.51	19.19**	1.81
6 Florets/Spike	717.49**	44.82	380.17**	46.97
7 Florets/cm	3.26**	0.24	4.67**	0.50
8 Kernels/Spike	1469.16**	80.11	248.50**	40.86
9 Fertility	0.38**	0.02	0.06**	0.01
10 Grain/Plant	47.85**	2.70	1.40**	0.30
11 Dry Weight/Plant	344.13**	20.64	39.51**	9.14
12 Harvest Index	0.19**	0.01	0.02**	0.003
13 Kernel Weight	7.30**	0.30	----	-----
14 Straw Protein	4.99**	0.30	1.13**	0.37
15 Grain Protein	7.71**	0.39	----	----

Hexaploid Triticale contained 14 plants in each of 21 lines.
Octoploid Triticale contained 10 plants in each of 27 lines.

* significant at the 5% level

**significant at the 1% level

TABLE 17. Mean square values and significance from the analysis of variance calculated on the means of each line for seven hexaploid and five octoploid triticales families

Character	Hexaploid Triticale	Error	Octoploid Triticale	Error
1 Days to Heading	95.01**	7.03	39.68*	13.71
2 Plant Height	233.50**	66.40	229.76**	43.27
3 Flag Leaf Length	9.84**	1.91	2.34	4.08
4 Spike Number	4.87**	0.48	1.87	0.97
5 Spike Length	6.78**	0.29	10.56**	2.11
6 Florets/Spike	158.66**	7.87	46.70	36.44
7 Florets/cm	0.64**	0.07	0.93	0.38
8 Kernels/Spike	217.94*	58.53	47.99	20.64
9 Fertility	0.06*	0.01	0.01	0.01
10 Grain/Plant	8.05**	1.49	0.27	0.12
11 Dry Weight/Plant	74.59**	3.70	2.75	4.17
12 Harvest Index	0.03*	0.01	0.004	0.002
13 Kernel Weight	8.63**	1.52	2.47	2.53
14 Straw Protein	6.63**	0.73	0.63	0.55
15 Grain Protein	6.86	2.56	3.60	3.50

Hexaploid Triticale contained 7 families

Octoploid Triticale contained 5 families

* significant at the 5% level

**significant at the 1% level

TABLE 18. Mean square values and significance from the analysis variance of the plant characteristics for the hexaploid triticale data within each family.

Character	1/	Error	2/	Error	3/	Error
1 Days to Heading	73.96**	3.64	162.71**	10.29	118.78**	9.61
2 Plant Height	290.46**	45.73	3419.54**	244.66	28.71	149.24
3 Flag Leaf Length	48.31	23.84	12.37	32.21	10.27	18.11
4 Spike Number	16.12**	2.79	0.48	0.50	2.60	1.41
5 Spike Length	3.01**	0.50	2.35	2.03	8.44**	1.68
6 Florets/Spike	41.14**	10.80	90.52	87.43	278.79**	45.52
7 Florets/cm	0.32**	0.09	1.02	0.62	0.31	0.16
8 Kernels/Spike	1691.94**	77.47	24.99	48.77	366.62*	92.77
9 Fertility	0.43**	0.02	0.01	0.01	0.09**	0.02
10 Grain/Plant	61.63**	6.68	0.11	0.19	7.36**	1.67
11 Dry Weight/Plant	119.46**	27.00	0.71	2.49	38.19	35.05
12 Harvest Index	0.16**	0.01	0.04	0.01	0.06**	0.01
13 Kernel Weight	5.04**	0.14	0.15	0.13	6.68**	0.28
14 Straw Protein	1.23*	0.24	3.41	0.66	0.75	0.14
15 Grain Protein	11.76**	0.11	2.26	0.33	1.17	0.40

1/ 'Jori' X Snoopy contained 14 plants in each of 5 lines
 2/ 'Jori' X 213 contained 14 plants in each of 4 lines
 3/ 'Jori' X 220 contained 14 plants in each of 4 lines

*significant at the 5% level

**significant at the 1% level

TABLE 18 - Concluded

Character	4/	Error	5/	Error	6/	Error
1 Days to Heading	31.60*	8.53	2.12	12.10	88.11*	4.04
2 Plant Height	168.17	133.70	72.77	400.27	43.06	134.11
3 Flag Leaf Length	0.60	19.01	78.89	19.35	30.56	12.54
4 Spike Number	9.02**	1.13	0.00	0.53	0.47	0.73
5 Spike Length	5.22**	0.87	1.25	2.69	0.01	2.07
6 Florets/Spike	2.79	22.50	19.05	64.28	197.04	62.55
7 Florets/cm	2.36**	0.15	0.36	0.41	2.05**	0.15
8 Kernels/Spike	1714.36**	112.91	70.60	80.47	2.93	95.19
9 Fertility	0.38**	0.02	0.02	0.02	0.00	0.02
10 Grain/Plant	11.68*	3.49	0.09	0.43	0.17	1.43
11 Dry Weight/Plant	64.75	21.71	0.06	7.16	0.24	8.66
12 Harvest Index	0.19**	0.01	0.02	0.01	0.02	0.02
13 Kernel Weight	0.70	0.42	0.30	1.06	0.20	0.25
14 Straw Protein	1.41*	0.07	0.12	0.46	0.00	0.35
15 Grain Protein	6.35*	0.24	1.32	1.57	0.42	0.45

4/ 'Jori' X 194 contained 14 plants in each of 3 lines
 5/ 'Jori' X 100 contained 14 plants in each of 2 lines
 6/ 'Jori' X 106 contained 14 plants in each of 2 lines

* significant at the 5% level
 ** significant at the 1% level

triticale families (Table 18) contained significantly different lines for a few of the characters measured. These results indicate that each rye line differed in its ability to produce uniform triticale lines with the tetraploid wheat. The results of the analyses of variance for the five octoploid triticale families (Table 19) contrasted with the above results for the six hexaploid triticale families. There was no apparent difference in the ability of the parental rye lines to produce significantly different triticale lines within each of the five octoploid triticale families for the characters measured.

The main points from these analyses are: (1) The results of the F-test revealed significant differences among the hexaploid and octoploid triticale lines. The genetic variation would allow selection for these characters among the triticale lines. (2) The results of the F-test of the second set of one-way analyses of variance indicated that some of the variation among the individual lines of hexaploid triticale was due to the variation among the parental ryes. This observation was not generally present among the octoploid triticales. (3) The results of the third analyses of variance of the hexaploid triticale illustrated the different degrees of variation which had been present in the different parental ryes. This observation was not present among the octoploid triticales.

TABLE 19. Mean square values and significance from the analysis of variance of the plant characteristics for the octoploid triticale data within each family.

Character	1/	Error	2/	Error	3/	Error
1 Days to Heading	201.45**	7.55	110.96**	13.04	67.65**	11.86
2 Plant Height	450.15**	70.70	563.58**	50.17	502.13**	93.30
3 Flag Leaf Length	34.51	11.32	50.07**	11.92	73.09**	18.26
4 Spike Number	12.91**	1.67	15.95**	3.39	9.93*	3.66
5 Spike Length	11.94**	1.79	11.40**	1.07	20.41**	1.68
6 Florets/Spike	117.43**	33.19	88.44**	24.63	558.63**	39.72
7 Florets/cm	1.76**	0.45	3.31**	0.45	7.21**	0.48
8 Kernels/Spike	116.39**	25.96	301.91**	24.09	422.17**	108.20
9 Fertility	0.02**	0.01	0.08**	0.01	0.08	0.03
10 Grain/Plant	0.63**	0.13	2.44**	0.22	1.80	0.94
11 Dry Weight/Plant	52.58**	8.87	46.59**	7.14	36.52	15.13
12 Harvest Index	0.01**	0.001	0.02**	0.002	0.04**	0.01
13 Kernel Weight	4.33*	1.11	3.42	1.09	3.21	0.63
14 Straw Protein	0.43	0.37	2.31	0.55	1.50	0.48
15 Grain Protein	1.74*	0.14	0.03	0.25	15.18*	1.70

1/ 'Sonora 64' X 199 contained 10 plants in each of 7 lines
2/ 'Sonora 64' X 2D82-S5 contained 10 plants in each of 6 lines
3/ 'Sonora 64' X 194 contained 10 plants in each of 5 lines

*significant at the 5% level
**significant at the 1% level

TABLE 19 - Concluded

Character	4/	Error	5/	Error
1 Days to Heading	215.08**	10.65	40.69	17.23
2 Plant Height	226.22	129.50	362.28*	105.21
3 Flag Leaf Length	41.86*	14.92	15.23	14.47
4 Spike Number	2.85	2.77	1.70	2.72
5 Spike Length	12.00**	2.14	2.57	2.70
6 Florets/Spike	800.55**	67.64	477.60**	87.80
7 Florets/cm	5.07**	0.67	2.65**	0.46
8 Kernels/Spike	96.57*	25.99	86.13*	26.53
9 Fertility	0.04**	0.01	0.02*	0.01
10 Grain/Plant	0.15	0.08	0.64*	0.17
11 Dry Weight/Plant	38.36**	7.21	23.04*	7.56
12 Harvest Index	0.01*	0.003	0.01*	0.001
13 Kernel Weight	3.35*	0.26	11.66**	0.61
14 Straw Protein	0.57	0.19	0.69	0.18
15 Grain Protein	5.30	0.54	5.85**	0.06

4/ 'Sonora 64' X Snoopy contained 10 plants in each of 5 lines

5/ 'Sonora 64' X 220 contained 10 plants in each of 4 lines

* significant at the 5% level

**significant at the 1% level

TABLE 20. Simple phenotypic correlation coefficients between pairs of characters for twenty-one hexaploid triticale lines.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Days to Heading														
2 Plant Height	-0.27													
3 Flag Leaf Length	-0.71**	0.26												
4 Spike Number	-0.83**	0.39	0.57*											
5 Spike Length	-0.71**	0.62**	0.37	0.75**										
6 Florets/Spike	-0.51*	0.55**	0.28	0.49*	0.85**									
7 Florets/cm	0.59**	-0.39	-0.27	-0.68**	-0.66**	-0.17								
8 Kernels/Spike	-0.60**	0.21	0.64**	0.40	0.31	0.12	-0.41							
9 Fertility	-0.56**	0.17	0.62**	0.37	0.25	0.03	-0.43*	0.99**						
10 Grain/Plant	-0.71**	0.24	0.71**	0.66**	0.47*	0.18	-0.59**	0.91**	0.91**					
11 Dry Weight/Plant	-0.81**	0.53*	0.57**	0.91**	0.92**	0.73**	-0.67**	0.42	0.36	0.64**				
12 Harvest Index	-0.39	0.03	0.54*	0.19	0.03	-0.17	-0.30	0.91**	0.94**	0.78**	0.12			
13 Kernel Weight	-0.73**	0.39	0.62	0.81**	0.66**	0.58**	-0.40	0.40	0.35	0.56**	0.77**	0.21		
14 Straw Protein	0.41	-0.37	-0.54*	-0.35	-0.16	0.12	0.47*	-0.82**	-0.84**	-0.74**	-0.26	-0.83**	-0.32	
15 Grain Protein	-0.29	0.03	-0.01	0.51*	0.29	0.14	-0.35	-0.36	-0.37	-0.11	0.40	-0.50*	0.34	0.31

* significant at the 5% level

** significant at the 1% level

2. Correlation Among Characters of Hexaploid Triticale

Simple correlation coefficients were calculated between each pair of characters measured on each line of hexaploid triticale. These correlations were based upon the mean of 14 measurements for each of twenty-one lines of hexaploid triticale (Table 20).

Days to heading showed significant negative correlations with flag leaf length, spike number, spike length, florets per spike, kernels per spike, fertility, grain per plant, dry weight per plant, and kernel weight. Straw protein was negatively correlated with flag leaf length and the characters measuring spike and plant grain production. Floret density (florets per cm) increased with days to heading and decreased with spike length and spike number per plant.

Plant height was positively correlated with spike length, florets per spike, and dry weight per plant. There was no relationship between any of the factors concerned with grain production and plant height.

The flag leaf length of hexaploid triticale showed a positive correlation with spike number, dry weight per plant and all characters concerned with spike or plant yield as well as kernel weight. Longer flag leaves were definitely associated with the bigger and more productive hexaploid triticale lines.

The number of spikes per plant and the spike length on the hexaploid triticale lines were positively correlated with each other, and with florets per spike, and dry weight per

plant. Spike number was also positively correlated with plant yield and kernel weight. The positive correlation between spike number and grain protein was the only positive correlation with grain protein for the characters measured in hexaploid triticales.

The number of florets per spike was positively correlated with dry weight per plant and kernel weight in addition to the correlations already mentioned. The capacity of the spike for grain production was not correlated with the actual grain production in the hexaploid triticales lines.

The number of kernels per spike, fertility, grain per plant, and harvest index were positively intercorrelated among the hexaploid triticales lines. These results pointed out the strong relationship among the characters measuring spike and plant grain production. This relationship occurred because the sterility caused most of the grain to be on the first tiller. In addition, fertility was positively correlated with dry weight per plant and harvest index was positively correlated with grain protein.

The above correlations among the characters of hexaploid triticales were dominated by the many significant correlations with days to heading, flag leaf length, and the intercorrelation among the four characters measuring spike and plant yield. The fourteen observations in each mean used for the calculations strengthened the validity of the correlation coefficients.

3. Correlations Among Characters of Octoploid Triticale

Simple phenotypic correlations were calculated among the fourteen characters of the octoploid triticale lines. The correlation coefficients between individual characters were based upon the mean of 10 measurements for each of twenty-seven lines of octoploid triticale (Table 21).

The number of days to heading, florets per cm, and straw protein were positively intercorrelated and negatively correlated with other plant characteristics. Octoploid triticale lines requiring more time to head had shorter flag leaves and fewer spikes per plant. Straw protein was negatively correlated with the characters measuring spike and plant yield as well as kernel weight. The number of florets per cm was negatively correlated with flag leaf length and spike length.

Spike length was positively correlated with the number of spikes per plant, kernel weight, and plant height among the octoploid triticale lines. Kernel weight was also positively correlated with the dry weight per plant. The number of florets per spike was positively correlated with flag leaf length and plant height among the octoploid triticale lines.

The number of kernels per spike, fertility, grain per plant, and harvest index were positively intercorrelated among the octoploid triticale lines. The strong relationship among the characters measuring spike and plant grain production for the octoploid triticale lines was the same as observed among the hexaploid triticale lines.

The correlation coefficients among the characters of

TABLE 21. Simple phenotypic correlation coefficients between pairs of characters for twenty-seven octoploid triticale lines.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13
1 Days to Heading													
2 Plant Height	0.36												
3 Flag Leaf Length	-0.62**	-0.15											
4 Spike Number	-0.64**	-0.16	0.38*										
5 Spike Length	0.09	0.58**	0.12	-0.17									
6 Florets/Spike	0.49**	0.59**	-0.40	-0.04	0.38*								
7 florets/cm	0.30	-0.22	-0.65**	-0.02	-0.56**	0.23							
8 Kernels/Spike	-0.24	0.14	0.21	0.06	0.14	0.17	-0.20						
9 Fertility	-0.04	0.00	0.09	0.04	0.14	0.28	-0.10	0.61**					
10 Grain/Plant	-0.32	0.16	0.21	0.20	0.10	0.21	-0.13	0.94**	0.60**				
11 Dry Weight/Plant	0.04	0.04	-0.21	0.09	-0.17	-0.03	0.19	-0.11	-0.11	-0.06			
12 Harvest Index	-0.27	-0.03	0.17	0.05	0.06	0.06	-0.16	0.96**	0.62**	0.92**	-0.11		
13 Kernel Weight	-0.31	0.36	-0.01	0.24	0.31	0.42*	-0.13	0.36	0.15	0.47*	0.11	0.31	
14 Straw Protein	0.45*	-0.16	-0.37	-0.32	-0.15	-0.07	0.44*	-0.58**	-0.42*	-0.64**	0.15	-0.55**	-0.53**

* significant at the 5% level

** significant at the 1% level

octoploid triticales were dominated by the strong intercorrelations among the four characters measuring spike and plant grain production. These characters were also consistently negatively correlated with straw protein.

DISCUSSION

The assessment of the effect of parental rye on the resulting amphidiploids when it is crossed onto wheat can be approached in at least two ways. First, a direct approach would be the comparison of the parental rye with the amphidiploid derived from it. The greatest drawback of this approach would be acquiring a large enough population of amphidiploids to make this comparison statistically valid. Most research programs are limited by time and space which necessitates a compromise between what is best and what is possible. As an example, this study began with fourteen rye parentals but ended with seven hexaploid and five octoploid triticales families. However, during the synthesis of the twelve triticales families, 1781 embryos were cultured onto media and 372 plants were treated with a colchicine solution for chromosome doubling. A direct approach would be a comparison between the seven or five triticales families and their respective parental rye lines. This sample would contain an insufficient number of comparisons for a statistically valid test.

A second approach, which was used in this study, involves the search for similar comparisons among parental rye lines and their top-cross rye lines and triticales hybrids. This study illustrated that individual rye parentals vary in their ability

to produce amphidiploids. In addition, those wheat-rye combinations which produced reproductive amphidiploids usually produced more than one line. Thus, each line of triticales originated from one doubled amphidiploid which traced back to a parental rye gamete. The second approach allowed each triticales line to be subjected to a separate statistical analysis separately rather than as the mean of all triticales lines from one rye parent. For the present data this was a study of hexaploid triticales with 21 lines and octoploid triticales with 27 lines.

The first section contains a discussion of the information acquired concerning triticales synthesis from wheat and rye parents. The second section contains a discussion of the occurrence of grass dwarfing and pericarp colour in rye and triticales. The third section deals with the amount of genetic variance among the lines of rye and triticales. The fourth section discusses the environmental effects on the plant characteristics and inbred and top-cross rye. The fifth section deals with the correlations between inbred and top-cross rye. The sixth section contains a discussion of the correlations among each of the characters in rye and triticales.

Synthesis Techniques

The difficulty associated with triticales synthesis from wheat and rye was amply demonstrated in the present study. A small proportion of the hexaploid wheat florets pollinated with rye pollen developed into amphidiploids (7% of embryos cultured).

The low seed-set on the cross (average of 4.3 per spike) compared favourably with the results of Riley and Chapman (1967) and Krolow (Kaltsikes, 1974). Forty-six percent of the octoploid embryos, which were large and well developed, reached maturity. This is similar to the results of Krolow (1970).

Tetraploid wheat ('Jori') crossed with diploid rye produced an average seed-set of 11.8 per spike which was comparable to the results of Riley and Chapman (1967) for their highly crossable tetraploid wheat. The embryos produced from 'Jori' by diploid rye were very small, poorly developed, and only 2% produced amphidiploids. The low survival rate appeared to be associated with poor embryo development. The low survival of tetraploid wheat-rye embryos also occurred in the material used by Krolow (1970).

The tetraploid embryos had begun development but failed to produce normal embryos. This arrest of embryo development was not the same as that described by Tozu (1966) where development stopped at fertilization. The embryos from the tetraploid 'Jori' appeared to cease growth due to a physiological blockage of the embryonic development after a successful fertilization.

The rate of chromosome doubling of the hexaploid triticale hybrids treated with 0.1% colchicine was 29% (Table 2). This figure was lower than the 46% doubling obtained by Sanchez-Monge (1958). However, this was most likely due to the fact that in the present study only one vial was used per plant whereas Sanchez-Monge (1958) had used one to three vials. The rate of doubling the octoploids was much lower (14%) than the

hexaploid triticales.

The present results may agree with those of Sanders and Hull (1970) and Subrahmanyam and Kasha (1975) even though these authors received a positive effect from addition of dimethyl sulfoxide. In the case of Rubus and barley haploids the colchicine plus dimethyl sulfoxide solution was effective on germinating seeds and very young seedlings. When colchicine and dimethyl sulfoxide solution was applied to the apices of older Rubus plants there was no benefit from the dimethyl sulfoxide. The technique of applying the colchicine and dimethyl sulfoxide solution to the apices of Rubus was similar to the technique used on triticales hybrids in the present study and produced the same results.

Grass Dwarfing and Pericarp Colour

1. Grass Dwarfing

The grass dwarf hybrids obtained from the three crosses with 'Sonora 64' resembled those described by Moore (1966). In contrast with the results presented by Fick and Qualset (1973b), grass dwarf hybrids were obtained from crosses with 'Sonora 64'. These results could be explained by a subsequent change in 'Sonora 64' or the interaction between the wheat and rye genomes. The different segregation patterns between crosses of Sonora 64 by inbred rye 199 and 385 indicated the definite contribution of the rye to the expression of the grass dwarfing. The segregation ratio from the crosses 'Sonora 64' by inbred 199 and by 2D82 self-fertile fit a 1:1 ratio. The

results indicated that the genetic factor in rye causing grass dwarfing was heterozygous in the inbred rye 199 and in 2D82 self-fertile but homozygous in inbred 385. The expression of grass dwarfing required the interaction of the wheat and rye genomes because no grass dwarfs appeared in the S₄ generations or top-crosses from the inbred line 199. Hermesen (1967) reviewed several papers which presented abnormal segregation ratios but these had not taken into account differential viability between dwarf and normal plants. Differential viability most likely did not occur in the present study because there was no visible difference between normal and grass dwarf hybrids until after the 2- to 3-leaf stage.

2. Pericarp Colour

The appearance of the purple pericarp colour in rye was similar to that described in tetraploid and hexaploid wheat by Sharman (1958) and Copp (1965). The segregation ratio among the inbred rye lines suggested a monofactorial inheritance pattern with the purple pericarp being dominant, similar to the situation reported by Sharman (1958). The results from three of the four top-cross populations also indicated that a single dominant gene, which had been heterozygous in the F₃ generation, was responsible for the pericarp colour.

The pericarp colour carried through into the hexaploid triticales but not into the octoploid triticales. The colour was uniform in intensity among the individuals of the hexaploid triticales families from inbred rye lines 100 and 106.

It was not uniform among the individual triticales plants from within and between the lines of triticales in the family from inbred rye 194. The intensity of the pericarp colour between the three lines of hexaploid triticales could have been caused by minor genes from the rye genome. However, the differences among genetically identical individuals of the triticales lines from inbred 194 must be due to some other factor such as gene expressivity.

Variance Components

The inbred parental rye lines used in this study contained readily detectable differences for the characters being measured. These differences undoubtedly arose because of the three generations of inbreeding and the different origins of the lines of rye. Similar analyses of variance among the top-cross rye lines, hexaploid triticales lines, and octoploid triticales lines indicated that an ample amount of variation was present for selection. The presence of genetic variation for the characters was similar to that found in studies in durum wheat (Amaya et al., 1972), hexaploid spring wheat (Hsu and Walton, 1970), and advanced lines of hexaploid triticales (Sethi and Singh, 1972; Gebremariam, 1974). Therefore, the results of the present analyses indicate that sufficient genetic variation existed among the inbred and top-cross lines of rye and among unselected amphidiploids at both ploidy levels to allow the possibility of selection for the characters measured.

Environmental Effects

The environmental effects can drastically alter the phenotypic expression of the plants. Therefore care must be taken to understand the response of each character to its environment. The calculations for the inbred and top-cross lines of rye in the present study give an evaluation of the response for each character to the field and growth cabinet conditions.

The change from growth cabinet to field conditions caused large increases in the means for spikes per plant, fertility, grain per plant, and dry weight per plant. These changes did not alter the presence of genetic variability among the lines of inbred and top-cross rye (Tables 8 and 9).

The effectiveness of selection for individual plant characteristics will depend upon the genetic inheritance and the environmental response of the character. The results of the F-tests for analyses of variance for replications of the rye field experiment indicated that four characters (flag leaf length, florets per spike, kernels per spike, and fertility) were not sensitive to the slight environmental differences between replications. The correlations for inbred and top-cross rye lines between similar and different environments gave an estimation of the ability of these lines of rye to maintain a similar ranking in different environments (Table 10). The correlations between environments indicated generally consistent rankings for seven of the inbred and top-cross rye lines (kernels per spike, fertility, grain per plant, harvest

index, florets per spike, kernel weight, and straw protein). These plant characteristics can be used for selection of rye lines with the assurance that there will be minimal interference of growth conditions. Selection for these characters can occur in one environment with the confidence that the selected lines will also be the best in the second environment.

Correlations between years for heading date in bread and durum wheat (Crumpacker and Allard, 1962) is analogous to the present comparison between different environments. Crumpacker and Allard (1962) generally found positive correlations between years for heading date in ten cultivars of hexaploid wheat. Kaltsikes and Lee (1973) found days to heading in ten cultivars of durum wheat failed to behave consistently over different environments. The present results indicated that days to heading was correlated between environments for the top-cross lines of rye ($r=0.69$) but not between the inbred lines ($r=0.45$).

Plant height and grain protein in the present study are extremely sensitive to changes in their growth conditions. Johnson et al. (1974) attributed most of the variation in seed protein to a response to the environment rather than to genetic origin. Improvement in plant height and grain protein would require information from many different locations to reduce the large environmental effect and allow the genetic variation to be expressed.

The sensitivity of plant and spike characteristics to

environmental changes can alter the results of simple correlation studies. Of the fifteen correlations in winter wheat (Fonseca and Patterson, 1968), two were significantly negative the first year and significantly positive the second year. The reversed correlations involved spikes per plot. The present experiments indicated that inbred and top-cross lines of rye were not correlated between different environments for spikes per plant which is a comparable character to spikes per plot. Despite the lack of correlation between different environments none of the correlations among the characters measured in any of the present experiments switched from a significantly positive to negative correlation (Tables 12, 13, 14, 15, 20 and 21).

Correlations Between Inbred and Top-Cross Rye

The significant correlations between inbred and top-cross rye lines demonstrated in this study, provides important information for the successful production of hybrid. The ability to select and breed for desirable traits in the inbred rye lines and have these desirable traits plus hybrid vigour in the resulting hybrids is a big advantage. Similar correlations were found in corn by Nanda (1966). Morgenstern and Geiger (1975) found that inbred rye line selection for hybridization could be based upon the top-cross rye performance. The results of the present correlations indicate that selection among the inbreds based upon inbred rye characteristics per se or upon top-cross rye characteristics, would produce the same results.

Similar correlations between inbred rye and triticales were not possible because of the restricted number of amphidiploids. However, the expression of rye characters (kernel colour and grass dwarf) in triticales suggested that these correlations exist between inbred rye and triticales. The correlations would be much weaker because the inbred rye genome would form a smaller proportion of the triticales chromosome constitution than in the top-cross hybrids and the sterility associated with new amphidiploids would distort the relationship between rye and triticales.

Correlations Among Plant Characteristics

The correlation coefficients between each pair of characters, in rye and triticales, fall into two basic categories. One group was formed by the intercorrelation of the four characters measuring spike and plant yield along with straw protein. The second group was formed by the intercorrelations of the characters measuring plant development (plant height, spike number, spike length, florets per spike, and dry weight per plant). The intercorrelations among the second group was weak but generally not correlated with the first group. This division occurred because inbred rye and new amphidiploids are meiotically less stable than advanced lines of triticales and wheat.

Spring wheat (Hsu and Walton, 1970 and 1971), winter wheat (Johnson et al., 1966a; Fonseca and Patterson, 1968) and advanced triticales lines (Gebremariam, 1974; Gustafson et al.,

1975; Sethi and Singh, 1972) contained many positive correlations between the agronomic characteristics (plant height, spike length, spike number, and spikelets per spike) and the reproductive characteristics (kernels per spike and plant or plot yield). The selection which had been applied to produce advanced lines and cultivars of wheat and triticales would also produce meiotically stable plants. In these plants the metabolites available for the synthesis of plant and grain characteristics have influenced the potential yield in accordance with the theory presented by Adams (1967). The lower fertility of the inbred ryes (Appendices I and II) and the triticales (Appendices III and IV) was most likely partly responsible for the lack of correlation between the agronomic development and yield. When the fertility of the rye and triticales lines is improved to the point where fertility is not the most limiting factor to the yield then the correlation between plant structure and yield will likely be present.

1. Days to Heading

The simple correlations between days to heading and the other characters measured in the triticales produced results similar to those obtained in spring wheat (Hsu and Walton, 1970 and 1971). The triticales and spring wheat with the shorter days to heading had a longer flag leaf and fewer florets per spike than those which headed later. Neither rye nor triticales lines have shown any correlation between days to heading and plant height but Hsu and Walton (1971) associated higher plant yield with moderately short but broad

flag leaves and a higher number of spikelets per spike. The only similarity between the present correlations regarding days to heading and those of Gebremariam (1974) was the negative correlation with kernel weight.

The days required for the triticale to head were associated with the type of plant produced. The late maturing plants contained fewer spikes but a denser and larger number of florets. The increased days to heading most likely caused the lower kernel weight and increased straw protein. All of the plants were harvested at the same time and the late maturing plants may not have been able to translocate as much photosynthate to the grain as the earlier maturing plants. This situation also occurred in the study of space planted spring wheat conducted by Syme (1972). The later and bigger plants produced smaller and fewer kernels per spike. The grain yield per plant in wheat had not been altered but because of the larger plants the harvest index was negatively correlated with days to spike emergence (Syme, 1972). Days to heading produced very inconsistent results among the inbred and top-cross ryes for the growth cabinet and field experiments. The data indicated a possible negative relationship with spike size and grain production among the inbred rye lines and with spike number among the top-cross rye lines.

2. Plant Height

There were no similarities between the significant correlations in rye and triticale in regards to plant height and

the other characters. Plant height was positively correlated with spike number, dry weight per plant and grain yield per plant in three of the four rye correlation studies (Tables 12 to 15 inclusive).

3. Flag Leaf Length

Hexaploid triticales flag leaf length was significantly correlated with eight characters (Table 20). Flag leaf length was positively correlated with the characters measuring plant size and grain production. In contrast, there was no consistent relationship between flag leaf length and any of the other characters measured on inbred and top-cross rye. The octoploid triticales contained two significant correlations but only the positive correlation with spike number occurred elsewhere in this study.

The results from hexaploid triticales differed from those in rye (Kaltsikes, 1973a) and wheat (Hsu and Walton, 1971) where there was no relationship between flag leaf length and grain yield. However, Hsu and Walton (1971) found positive correlations between flag leaf length and the characters kernels per spike, and kernel weight. The positive relationship between flag leaf length and the other characters may prove to be an easy selection tool for yield improvements but it is restricted to the hexaploid triticales.

4. Spike Number and Dry Weight per Plant

These characters are discussed together because of the consistent association with one another. Spike number and dry

weight per plant were generally positively intercorrelated and correlated with grain per plant in the rye and hexaploid triticales experiments. The present correlations were in agreement with those between spike number per plant or per meter of row and yield obtained in spring rye (Kaltsikes, 1973a), spring wheat (Fischer and Kertesz, 1976) and in advanced lines of hexaploid triticales (Gebremariam, 1974; Sethi and Singh, 1972). Fischer (1973) and Syme (1972) observed a positive relationship between spike number and days to maturity in contrast to the negative relationship for the comparable correlation in the present study. The triticales grown in the growth cabinets tended to produce a second growth of tillers on those plants which headed early and this could explain the negative relationship.

5. Spike Length and Florets per Spike

These two characters were correlated among the inbred rye and triticales lines. A significant positive correlation between the spike length and spike yield of parental rye lines was obtained in the growth cabinet and the hexaploid triticales lines contained a positive correlation between spike length and plant yield. These limited results contrast with a study by Syme (1972) who failed to find any association between spike length and spike or plant yield. Thus, the relationship between spike length and yield experienced by Gebremariam (1974) and as expected by Larter (1973) and Fischer (1973) did occur in the hexaploid triticales but not consistently in the rye lines.

Florets per spike was positively correlated with kernel weight for both ploidy levels of triticales but not for any of the rye. This may prove to be a useful selection index among the triticales.

6. Florets per cm

The floret density (florets per cm) was correlated with other characters only among the hexaploid triticales. These correlations can conveniently be grouped with days to heading and straw protein because these were the characters generally negatively correlated with the rest of the characters in this study. A dense spike, among the hexaploid triticales lines, was associated with a smaller plant which produces less grain (Table 20).

7. Kernels per Spike, Fertility, Grain per Plant, and Harvest Index

The number of kernels per spike, fertility, and harvest index were intercorrelated in all experiments of rye and triticales. Grain per plant and harvest index were also correlated in rye and triticales experiments. The results of the correlations between each pair of these four characters in triticales differed from those in rye in that grain per plant was not correlated with the other three characters in rye. The correlation between plant yield and spike yield among the triticales arose because of the sterility among the triticales lines. Most of the grain on the triticales plants was on the first tiller and thus this tiller had a major influence on the plant yield. The present triticales

results agree with those in bread wheat (Syme, 1972) where grain yield per plant was positively correlated with kernels per spike in a greenhouse study.

8. Kernel Weight

Kernel weight was independent of all other characters in the four rye experiments. In contrast, the hexaploid triticales lines were positively correlated between kernel weight and the characters measuring plant size and plant grain yield. The positive correlation between kernel weight and plant yields was similar to that of winter wheat (Fonseca and Patterson, 1968) and spring wheat (Hsu and Walton, 1970; Fischer and Kertesz, 1976). The negative association which occurred in wheat between the components of yield, kernel weight with spike number (Fonseca and Patterson, 1968; Syme, 1972; Hsu and Walton, 1971) and kernel weight with kernels per spike (Fonseca and Patterson, 1968; Hsu and Walton, 1970) did not occur in the triticales or rye lines. Thus the wide spread negative association between the components of yield of the major crop plants (Adams, 1967) does not always occur. The general lack of negative correlations among the components of yield in the triticales lines most likely occurred because of the low fertility which did not allow the demand for photosynthate to reach or exceed the available supply.

9. Straw Protein

Straw protein was consistently negatively correlated with fertility and grain yield per plant in the growth cabinet

experiments of rye and triticale. The triticales results from both ploidy levels showed negative correlations between the characters measuring spike and plant yield with straw protein. Straw protein was positively correlated with days to heading in the octoploid triticale in agreement with a study by Campbell and Frey (1974) in oats. The negative correlation between straw and grain protein observed in wheat (Johnson et al., 1967) did not occur in any of the present experiments.

10. Grain Protein

Grain protein failed to produce any consistent correlations among the rye lines or hexaploid triticale lines. The two correlations which did occur were both negative with fertility and harvest index. Protein selection could not be predicted from any of the other characters in rye or hexaploid triticale.

CONCLUSION

It is possible to select for certain desirable triticales characteristics from among parental rye lines. One of the reproductive characteristics (kernels per spike, fertility, or harvest index), kernel weight, and florets per spike are the plant characteristics which have the greatest potential as selection indices. This conclusion is based upon the following facts emanating from this study.

Variance Components

The results of the F-tests indicated that there were significant differences among the inbred rye lines in the growth cabinet and field experiments for the characters measured. The existence of genetic variation among the parental rye lines was essential if genetic differences were to be observed among the hybrids produced from these lines.

The genetic differences present in the inbred rye lines carried into the top-cross rye lines grown in the growth cabinet and field experiments. The significant F-tests for all but one of the characters indicates the presence of the genetic variation in the top-cross lines grown in both environments.

The triticales at each ploidy level were genetically identical except for the seven chromosomes contributed by the parental rye. Despite the close genetical relationship

among the triticales lines, the twenty-one hexaploid and the twenty-seven octoploid triticales lines contained significantly different lines for each of the fifteen characters. The individual parental rye line influenced the number of characters for which the hexaploid triticales family contained significantly different lines. Overshadowing the inbred rye lines contribution to each individual line of hexaploid triticales was the variation among the families of triticales. Thus, a great deal of the genetic variation among the hexaploid triticales lines was associated with the genetic variation between parental rye lines.

The lines of triticales within each family of octoploid triticales contained differences for many of the characters. However, the variation among the octoploid triticales lines was not associated with parental rye lines. The greater part of the genetic variation among the individual octoploid triticales lines could have been caused by an additional factor such as chromosome instability or chromosome loss.

Environmental Effects

The environmental conditions did not greatly alter the rankings of the inbred and top-cross rye lines for the number of florets per spike, kernels per spike, fertility, days to heading, harvest index, kernel weight, and straw protein. The use of any of these seven characters as selection indices among the rye lines would produce similar results in either environment.

Correlations Between Inbred and Top-Cross Rye

The positive correlation between inbred and top-cross lines of rye for many of the fifteen characters studied indicated the direct influence of the inbred rye lines on their top-cross hybrids. The number of spikes per plant, florets per spike, kernels per spike, fertility, harvest index, and kernel weight were positively correlated between inbred and top-cross lines of rye in both environments.

Correlations Among Plant Characteristics

The performance of the parental rye lines was shown to be associated with that of their hybrids by the results of the correlation studies between each pair of characters. The following correlations between plant characteristics occurred within parental rye lines as well as within the lines of hybrids derived from the parental rye lines.

(a) The characters measuring grain production (kernels per spike, fertility, and harvest index) were generally inter-correlated among the inbred rye, top-cross rye, hexaploid triticales, and octoploid triticales lines.

(b) Straw protein was negatively correlated with fertility and harvest index among the inbred and top-cross rye lines grown in the growth cabinet as well as among the hexaploid and octoploid triticales lines. Straw protein was also negatively correlated with kernels per spike and grain per plant among the triticales lines at both ploidy levels.

(c) Spike number was positively correlated with dry

weight per plant in all experiments except octoploid triticales. Spike number was related to grain per plant in three of the four rye experiments and the hexaploid triticales experiment.

(d) Plant height was positively correlated with spike number, grain per plant, and dry weight per plant among the rye lines but not the triticales lines. Both ploidy levels of triticales contained a positive correlation between plant height and the characters spike length and florets per spike.

(e) Days to heading was negatively correlated with spike length and grain production characters among the inbred lines of rye in the growth cabinet and the hexaploid triticales lines. These negative correlations were not obtained in the other three sets of rye correlations nor in the octoploid triticales correlations.

The intercorrelations among the characters measuring grain production and plant development indicated that only one character need be measured to represent each trait. The characters measuring grain production (kernels per spike, fertility, and harvest index) were found to be environmentally stable and were correlated between inbred and top-cross ryes.

The characters measuring plant development (spike number, dry weight per plant, and plant height) were not environmentally stable and were not consistently correlated between populations of ryes. These characters would not be very reliable as selection indices under the present conditions of experimentation.

Kernel weight and the number of florets per spike would each prove to be good selection indices because of their lack

of correlation with other characters, their environmental stability, and their correlation between inbred and top-cross rye lines.

Relationship Between Rye and Triticale Amphidiploids

This study presents many indications that the rye parent does affect the phenotypic expression of the triticale produced from it. These points are:

1. the transfer of the rye pericarp colour into the triticale lines.
2. the required presence of the rye genome for the expression of grass dwarf mutant.
3. the transfer of genetic variability for the fifteen plant characteristics from the rye parent to the triticale lines.
4. the correlation between inbred and top-cross rye lines which suggests that this relationship may also exist between inbred rye and triticale.
5. the correlation coefficients between each pair of characteristics for the parental rye and triticale were either significant or non-significant for many of the same comparisons. Thus, the interrelationships among the various rye characteristics also exist among those expressed in the triticale synthesized from these ryes.

LIST OF REFERENCES

- ADAMS, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean. *Crop Science* 7:505-510.
- ALLAN, R. E. and VOGEL, O. A. 1963. F₂ monosomic analysis of culm length in wheat involving semidwarf Norin 10-Brevor 14 and the Chinese Spring series. *Crop Science* 3:538-540.
- ALLAN, R. E., VOGEL, O. A. and PETERSON, C. J. JR. 1968. Inheritance and differentiation of semidwarf culm length of wheat. *Crop Science* 8:701-04.
- AMAYA, A. A., BUSCH, R. H. and LEBSOCK, K. L. 1972. Estimates of genetic effects of heading date, plant height, and grain yield in Durum wheat. *Crop Science* 12:478-481.
- BELL, G. D. H. 1950. Investigations in the Triticinae: I Colchicine techniques for chromosome doubling in interspecific and intergeneric hybridization. *J. Agric. Sci.* 40:9-18.
- BENNETT, M. D. 1973. Meiotic, gametophytic and early endosperm development in triticales. *Triticales: Proc. Int. Symp. (El Batan, Mexico)* pages 137-148.
- BENNETT, M. D. and KALTSIKES, P. J. 1973. The duration of meiosis in a diploid rye, a tetraploid wheat and a hexaploid triticales derived from them. *Can. J. Genet. Cytol.* 15:671-679.
- BHATT, G. M. 1972. Inheritance of heading date, plant height, and kernel weight in two spring wheat crosses. *Crop Science* 12:95-98.
- BOYD, W. J. R., SISODIA, N. S. and LARTER, E. N. 1970. A comparative study of the cytological and reproductive behaviour of wheat and triticales subjected to two temperature regimes. *Euphytica* 19:490-497.
- BROWN, C. M., ARYEETREY, A. N. and DUBEY, S. N. 1974. Inheritance and combining ability for oil content in oats (*Avena sativa* L). *Crop Science* 14:67-69.
- BROWN, C. M., WEIBEL, R. O. and SEIF, R. D. 1966. Heterosis and combining ability in common winter wheat. *Crop Science* 6:382-383.

- CAMPBELL, A. R. and FREY, K. J. 1974. Inheritance of straw protein content and its association with other traits in interspecific oat crosses. *Euphytica* 23:369-376.
- CHAPMAN, S. R. and MCNEAL, F. H. 1971. Gene action for yield components and plant height in a spring wheat cross. *Crop Science* 11:384-386.
- COPP, L. G. L. 1965. Purple grain in hexaploid wheat. *Wheat Inf. Ser.* 19,20:18.
- CRUMPACKER, D. W. and ALLARD, R. W. 1962. A diallel cross analysis of heading date in wheat. *Hilgardia* 32:275-318.
- DARVEY, N. L. 1973. Genetics of seed shrivelling in wheat and triticale. *Proc. 4th Int. Wheat Genet. Symp.* pages 155-159.
- DAVIS, W. H., MIDDLETON, G. K. and HERBERT, T. T. 1961. Inheritance of protein, texture, and yield in wheat. *Crop Science* 1:235-238.
- DEDIO, W., SIMMONDS, D. H., HILL, R. D. and SHEALY, H. 1975. Distribution of amylase in the triticale kernel during development. *Can. J. Plant Sci.* 55:29-36.
- FICK, G. N. and QUALSET, C. O. 1973a. Genes for dwarfism in wheat, *Triticum aestivum* L. *Genetics* 75:531-539.
- FICK, G. N. and QUALSET, C. O. 1973b. Inheritance and distribution of grass dwarfing genes in short-statured wheat. *Crop Science* 13:31-33.
- FISCHER, R. A. 1973. Agronomy and physiology of triticale. *Triticale: Proc. Int. Symp. (El Batán, México)* pages 137-148.
- FISCHER, R. A. and KERTESZ, Z. 1976. Harvest index in spaced populations and grain weight in microplots as indicators of yielding ability in spring wheat. *Crop Science* 16:55-59.
- FONSECA, S. and PATTERSON, F. L. 1968. Yield component heritabilities and interrelationships in winter wheat (*Triticum aestivum* L.). *Crop Science* 8:614-617.
- GEBREMARIAM, H. 1974. Relationship of agronomic and quality characteristics to yield of triticale. Ph. D. Thesis, Univ. of Manitoba, Winnipeg.
- GENTER, C. F. and ALEXANDER, M. W. 1966. Development and selection of productive S1 inbred lines of corn (*Zea mays* L.). *Crop Science* 6:429.
- GRAFIUS, J. E. 1956. Components of yield in oats: a geometrical interpretation. *Agronomy J.* 48:419-423.

- GRAFIUS, J. E. 1972. Competition for environmental resources by component characters. *Crop Science* 12:364-367.
- GUSTAFSON, J. P. 1973. Production of triticales germplasm. *Triticales: Proc. Int. Symp. (El Batan, Mexico)* pages 227-233.
- GUSTAFSON, J. P., QUALSET, C. O. and RUPERT, J. A. 1973. Registration of UC-90 dwarf rye germplasm. *Crop Science* 13:131-132.
- GUSTAFSON, J. P. and QUALSET, C. O. 1975. Genetics and breeding of 42-chromosome triticales II. Relations between chromosomal variability and reproductive characters. *Crop Science* 15: 810-813.
- GYAWALI, K. K., QUALSET, C. O. and YAMAZAKI, W. T. 1968. Estimates of heterosis and combining ability in winter wheat. *Crop Science* 8:322-324.
- HALLORAN, G. M. 1974. Genetic analysis of hexaploid wheat *Triticum aestivum* using intervarietal chromosome substitution lines. I Culm length, ear density, spikelet number, and fertility. *Can. J. Genet. Cytol.* 16:449-456.
- HALLORAN, G. M. 1975. Genetic analysis of time to ear emergence in hexaploid wheat, *Triticum aestivum*, using intervarietal chromosome substitution lines. *Can. J. Genet. Cytol.* 17:365-373.
- HERMSEN, J. G. TH. 1967. Hybrid dwarfness in wheat. *Euphytica* 16:134-162.
- HILL, R. D., KLASSEN, A. J. and Dedio, W. 1973. Metabolic factors influencing kernel development in triticales. *Triticales: Proc. Int. Symp. (El Batan, Mexico)* pages 149-154.
- HSAM, S. L. K. and LARTER, E. N. 1973. Identification of cytological and agronomic characters affecting the reproductive behaviour of hexaploid triticales. *Can. J. Genet. Cytol.* 15: 197-204.
- HSAM, S. L. K. and LARTER, E. N. 1974. Effects of inbreeding on triticales selected for two levels of fertility and chiasma frequency. *Crop Science* 14:213-215.
- HSU, C. S. and SOSULSKI, F. W. 1969. Inheritance of protein content and sedimentation value in diallel crosses of spring wheat (*Triticum aestivum* L.). *Can. J. Genet. Cytol.* 11: 967-976.
- HSU, P. and WALTON, P. D. 1970. The inheritance of morphological and agronomic characters in spring wheat. *Euphytica* 19:54-60.

- HSU, P. and WALTON, P. D. 1971. Relationships between yield and its components and structures above the flag leaf node in spring wheat. *Crop Science* 11:190-193.
- HURD, E. A. 1959. Inheritance of blue kernel colour in wheat. *Can. J. Plant Sci.* 39:1-8.
- HURD, E. A. and MCGINNIS, R. C. 1958. Note on the location of genes for dwarfing in Redman wheat. *Can. J. Plant Sci.* 38:506.
- JENKINS, M. T. 1929. Correlation studies with inbred and crossbred strains of maize. *J. Agric. Res.* 39:677-721.
- JENKINS, M. T. 1940. The segregation of genes affecting yield of grain in maize. *J. Amer. Soc. Agron.* 32:55-63.
- JENKINS, M. T. and BRUNSON, A. M. 1932. Methods of testing inbred lines of maize in crossbred combinations. *J. Amer. Soc. Agron.* 24:523-530.
- JOHNSON, V. A., BIEVER, K. J., HAUNOLD, A. and SCHMIDT, J. W. 1966a. Inheritance of plant height, yield of grain, and other plant and seed characteristics in a cross of hard red winter wheat, *Triticum aestivum* L. *Crop Science* 6:336-338.
- JOHNSON, V. A., SCHMIDT, J. W. and MEKASHA, W. 1966b. Comparison of yield components and agronomic characteristics of four winter wheat varieties differing in plant height. *Agron. J.* 58:438-441.
- JOHNSON, V. A., MATTERN, P. J. and SCHMIDT, J. W. 1967. Nitrogen relations during spring growth in varieties of *Triticum aestivum* L. differing in grain protein content. *Crop Science* 7:664-667.
- JOHNSON, V. A., MATTERN, P. J., SCHMIDT, J. W. and STROIKE, J. E. 1974. Genetic advances in wheat protein quantity and composition. *Proc. 4th Int. Wheat Genet. Symp.* pages 547-556.
- JONES, I. T. and HAYES, J. D. 1967. The effect of seed rate and growing season on four oat cultivars. I. Grain yield and its components. *J. Agric. Sci., Camb.* 69:103-109.
- KALTSIKES, P. J. 1971. The mitotic cycle in an amphidiploid (Triticale) and its parental species. *Can. J. Genet. Cytol.* 13:656-662.
- KALTSIKES, P. J. 1972. Duration of the mitotic cycle in triticale. *Caryologia* 25:537-542.
- KALTSIKES, P. J. 1973a. Multivariate statistical analysis of yield, its components and characters above the flag leaf node in spring wheat. *Theoret. Appl. Genet.* 43:88-90.

- KALTSIKES, P. J. 1973b. Univalency to triticales. Triticale: Proc. Int. Symp. (El Batan, Mexico) pages 159-167.
- KALTSIKES, P. J. 1974. Methods for triticales production. Z. Pflanzenzuchtg 71:264-286.
- KALTSIKES, P. J. and LEE, J. 1973. The genetic system controlling yield and related characters in durum yield. Proc. 4th Int. Wheat Genet. Symp. pages 533-540.
- KAUL, A. K. and SOSULSKI, F. W. 1965. Inheritance of flour protein content in a Selkirk X Gabo cross. Can. J. Genet. Cytol. 7:12-17.
- KEMPANNA, C. and SEETHARAM, A. 1972. Studies into meiotic stability, pollen and seed fertility in triticales. Cytologia 37:327-333.
- KETATA, H., EDWARDS, L. H. and SMITH, E. L. 1976. Inheritance of eight agronomic characters in a winter wheat cross. Crop Science 16:19-22.
- KLASSEN, A. J. and HILL, R. D. 1971. Comparison of starch from triticales and its parental species. Cereal Chem. 48: 647-654.
- KNOTT, D. R. 1958. The inheritance in wheat of a blue endosperm color derived from Agropyron elongatum ($2n=72$). Can. J. Botany 36:571-574.
- KNOTT, D. R. and TALUKDAR, B. 1971. Increasing seed weight in wheat and its effects on yield, yield components, and quality. Crop Science 11:280-283.
- KOBYLANSKI, V. D. 1975. Effect of the dominant character of short straw on some quantitative characters of winter rye. Eucarpia Conference on Rye Breeding (Poland, 1974) pages 495-501.
- KROLOW, K. D. 1970. Untersuchungen über die Kreuzbarkeit zwischen Weizen und Roggen. Z. Pflanzenzüchtg. 64:44-72.
- KRONSTAD, W. E. and FOOTE, W. H. 1964. General and specific combining ability estimates in winter wheat (*Triticum aestivum* Vill., Host) Crop Science 4:616-619.
- KUSPIRA, J. and UNRAU, J. 1957. Genetic analysis of certain characters in common wheat using whole chromosome substitution lines. Can. J. Plant Sci. 37:300-326.
- LARTER, E. N. 1973. Progress in the development of triticales in Canada. Proc. Int. Symp. (El Batan, Mexico) Pages 69-74.

LARTER, E. N. and SHIGENAGA, S. 1971. Further evidence on the derivation of univalents in hexaploid triticales. *Can. J. Genet. Cytol.* 13:895-898.

LARTER, E. N., TSUCHIYA, T. and EVANS, L. E. 1968. Breeding and cytology of triticales. *Proc. 3rd Int. Wheat Genet. Symp.* pages 213-221.

LEBSOCK, K. L., FIFIELD, C. C., GURNEY, G. M. and GREENAWAY, W. T. 1964. Variation and evolution of mixing tolerance, protein content and sedimentation value in early generations of spring wheat. *Triticum aestivum* L. *Crop Science* 4:171-174.

LEE, J. and KALTSIKES, P. J. 1972. Diallel analysis of correlated sequential characters in durum wheat. *Crop Science* 12:770-772.

LONNQUIST, J. H. and LINDSEY, M. F. 1964. Top cross versus S1 line performance in corn (*Zea mays* L.). *Crop Science* 4:580-584.

MCDANIEL, R. G. 1973. Mitochondrial complementation: A plant-breeding tool for estimating combining ability of wheats and triticales. *Proc. 4th Int. Wheat Genet. Symp.* pages 541-546.

McNEAL, F. H., BORG, M. A., McGUIRE, C. F., STEWART, V. R. and Baldridge, D. E. 1972. Grain and plant nitrogen relationships in eight spring wheat crosses, *Triticum aestivum* L. *Crop Science* 7:599-602.

MERKER, A. 1971. Cytogenetic investigations in hexaploid triticales. I. Meiosis, aneuploidy and fertility. *Hereditas* 68:281-290.

MERKER, A. 1973a. Identification of aneuploids in a line of hexaploid triticales. *Hereditas* 74:1-6.

MERKER, A. 1973b. Cytogenetics of hexaploid triticales. *Triticales*; *Proc. Int. Symp. (El Batan, Mexico)* pages 169-172.

MERKER, A. 1973a. Cytogenetic investigations in hexaploid triticales. II Meiosis and fertility in F1 and F2. *Hereditas* 73:285-290.

MOORE, K. 1969. The genetical control of the grass dwarf phenotype in *Triticum aestivum* L. *Euphytica* 18:190-203.

MORGENSTERN, K. and GEIGER, H. H. 1975. General and specific combining ability in test crosses between inbred lines of rye. *Eucarpia Conference on Rye Breeding (Poland, 1974)* pages 386-390.

- MORRISON, R. 1975. The genetics of resistance to Puccinia graminis tritici in hexaploid triticale. Ph.D. Thesis, Univ. of Manitoba, Winnipeg.
- MUNTZING, A. 1939. Studies on the properties and the ways of production of rye-wheat amphidiploids. Hereditas 25:387-430.
- MUNTZING, A. 1957. Cytogenetic studies in rye-wheat (Triticale). Proc. Int. Genet. Symp. (Tokyo, 1956) pages 51-56.
- MUNTZING, A. 1963. Cytogenetic and breeding studies in triticale. Proc. 2nd Int. Wheat Genet. Symp. pages 291-300.
- MUNTZING, A. 1973. Experiences from work with octoploid and hexaploid rye-wheat. Biol. Abs. 55(9):467448.
- NANDA, D. L. 1966. Evaluation of eight inbred lines of maize (Zea mays L.). Crop Science 6:67-69.
- NASS, H. G. 1973. Determination of characters for yield selection in spring wheat. Can. J. Plant Sci. 53:755-762.
- NICKELL, C. D. and GRAFIUS, J. E. 1969. Analysis of a negative response to selection for high yield in winter barley, Hordeum vulgare L. Crop Science 9:447-451.
- PLARRE, W. and FISCHER, V. 1975. Analysis of a diallel cross in inbred lines of rye. Eucarpia Conference on Rye Breeding (Poland, 1974) pages 391-401.
- QUINONES, M. A., LARTER, E. N., and SAMBORSKI, D. J. 1972. The inheritance of resistance to Puccinia recondita in hexaploid triticale. Can. J. Genet. Cytol. 14:495-505.
- RASMUSSEN, D. C. and CANNELL, R. Q. 1970. Selection for grain yield and components of yield in barley. Crop Science 10:51-54.
- REDDI, M. V., HEYNE, E. G. and LIANG, G. H. L. 1969. Heritabilities and interrelationships of shortness and other agronomic characters in F3 and F4 generations of two wheat crosses (Triticum aestivum L.). Crop Science 9:222-225.
- RILEY, R. and CHAPMAN, V. 1957. The comparison of wheat-rye and wheat-aegilops amphidiploids. J. Agric. Sci. 49:246-250.
- RILEY, R. and CHAPMAN, V. 1967. The inheritance in wheat of crossability with rye. Genet. Res. 9:259-267.
- RILEY, R. and MILLER, T. E. 1970. Meiotic chromosome pairing in triticale. Nature 227:82-83.
- ROMERO, G. E. and FREY, K. J. 1973. Inheritance of semidwarfness in several wheat crosses. Crop Science 13:334-337.

- ROUPAKIAS, D. G. and KALTSIKES, P. J. 1976a. The effect of the wheat cytoplasm on the meiosis of hexaploid triticales. *Can. J. Genet. Cytol.* (in press)
- ROUPAKIAS, D. G. and KALTSIKES, P. J. 1976b. The relation between duration of meiosis and chromosome pairing. (in press)
- RUPERT, E. A., RUPERT, J. A. and BEATTY, K. D. 1973. Cytological selection for fertility among triticales. *Proc. 4th Int. Wheat Genet. Symp.* pages 259-264.
- SANCHEZ-MONGE, E. 1959. Hexaploid triticales. *Proc. 1st Int. Wheat Genet. Symp.* pages 181-194.
- SANDERS, H. and HULL, J. W. 1970. Dimethyl sulfoxide as an adjuvant of colchicine in the treatment of *Rubus* seeds and shoot apices. *Hort. Sci.* 5:111-112.
- SETHI, G. C. and SINGH, H. B. 1972. Interrelationship of quantitative traits with grain yield in triticales. *Ind. J. Agr. Sci.* 42:281-285.
- SHARMAN, B. C. 1958. Purple pericarp: a monofactorial dominant in tetraploid wheats. *Nature* 181:929.
- SHEALY, H. E. and SIMMONDS, D. H. 1973. The early developmental morphology of the triticales grain. *Proc. 4th Int. Wheat Genet. Symp.* pages 265-270.
- SHEBESKI, L. H. 1958. Speculations on the impact of the D genome. *Proc. 1st Int. Wheat Genet. Symp.* pages 237-471.
- SHIGENAGA, A., LARTER, E. N. and MCGINNIS, R. C. 1971. Identification of chromosomes contribution to aneuploidy in hexaploid triticales cultivar Rosner. *Can. J. Genet. Cytol.* 13:592-596.
- SISODIA, N. S. and MCGINNIS, R. C. 1970. Importance of hexaploid wheat germ plasm in hexaploid triticales breeding. *Crop Science* 10:161-162.
- SPRAGUE, G. F. 1939. An estimation of the number of top-crossed plants required for adequate representation of a corn variety. *J. Amer. Soc. Agron.* 31:11-15.
- SPRAGUE, G. F. 1946. Early testing of inbred lines of corn. *J. Amer. Soc. Agron.* 38:108-117.
- SUBRAHMANYAN, N. C. and KASHA, K. J. 1975. Chromosome doubling of barley haploids by nitrous oxide and colchicine treatment. *Can. J. Genet. Cytol.* 17:573-583.

SUN, P. L. F., SHANDS, H. L. and FORSBERG, R. A. 1972. Inheritance of kernel weight in six spring wheat crosses. *Crop Science* 12:1-5.

ST. JOHN, R. R. 1934. A comparison of reciprocal top crosses in corn. *J. Amer. Soc. Agron.* 26:721-724.

SYME, J. R. 1972. Single-plant characters as a measure of field plot performance of wheat cultivars. *Aust. J. Agric. Res.* 23:753-760.

THOMAS, J. B. and KALTSIKES, P. J. 1971. Chromosome pairing in hexaploid triticale. *Can. J. Genet. Cytol.* 13:621-624.

THOMAS, J. B. and KALTSIKES, P. J. 1972. Genotypic and cytological influences on the meiosis of hexaploid triticale. *Can. J. Genet. Cytol.* 14:889-898.

TSUCHIYA, T. 1972. Variation of chromosome numbers in different seed size classes of hexaploid triticale. *Wheat Inf. Serv.* 33, 34:22-24.

TSUCHIYA, T. and LARTER, E. N. 1968. Direct synthesis of triticale from colchicine-doubled parents. *Can. J. Genet. Cytol.* 10:770.

VOLDENG, H. D. and SIMPSON, G. M. 1967. The relationship between photosynthetic area and grain yield per plant in wheat. *Can. J. Plant Sci.* 47:359-365.

WATKINS, R. and WHITE, W. J. 1964. The inheritance of anthocyanins in rye (*Secale cereale* L). *Can. J. Genet. Cytol.* 6:403-410.

WEIMARCH, A. 1973. Cytogenetic behaviour in octoploid triticale. I Meiosis, aneuploidy and fertility. *Hereditas* 74:103-118.

WEIMARCH, A. 1975. Kernel size and frequency of euploids in octoploid triticale. *Hereditas* 80:69-72.

WIDNER, J. N. and LEBSOCK, K. L. 1973. Combining ability in durum wheat: I Agronomic characteristics. *Crop Science* 13:164-167.

ZILLINSKY, F. J. 1973a. Improving seed formation in triticales. *Triticale: Proc. Int. Symp. (El Batan, Mexico)* pages 155-157.

ZILLINSKY, F. J. 1973b. The triticale improvement program at CIMMYT. *Triticale: Proc. Int. Symp. (El Batan, Mexico)* pages 81-85.

ZILLINSKY, F. J. and BORLAUG, N. E. 1971. Progress in developing triticale as an economical crop. Res. Bull. No. 17.

ZITTELLI, G. and MARIANI, B. M. 1973. Relationships between dwarfness (Norin 10) and agronomic traits in durum wheat used in breeding work. Proc. 4th Int. Wheat Genet. Symp. pages 617-623.

APPENDIX I. Plant numbers and means for fifteen characters in the rye experiment grown in the field

Rye	Days to Heading		Plant Height		Flag Leaf Length		Spike Number		Spike Length		Florets/Spike		Florets/cm		Kernels/Spike	
Inbred 199	63	60.4	63	88.0	60	9.47	63	7.1	63	9.56	63	57.8	63	6.13	63	28.7
Inbred 213	64	57.3	64	77.9	57	9.51	64	7.2	64	8.42	64	48.2	64	5.76	64	21.1
Inbred 277	62	61.1	62	95.4	59	9.23	62	10.4	62	9.20	62	47.2	62	5.17	62	12.5
Inbred 194	64	59.8	64	105.7	60	11.08	64	8.7	64	9.37	64	53.4	64	5.85	64	35.9
Inbred 2D82-S5	64	59.3	64	80.4	56	11.95	64	5.2	64	9.27	64	47.5	64	5.17	64	28.8
Inbred 100	59	60.2	59	74.8	57	9.01	59	4.8	59	7.98	59	42.3	59	5.35	59	17.6
Inbred 106	63	58.2	62	81.2	60	11.90	63	6.0	63	10.06	63	55.7	63	5.61	63	24.7
Inbred 195	61	54.5	62	99.9	51	9.17	62	10.9	62	8.62	62	48.3	62	5.62	62	20.8
Inbred 220	64	63.5	64	82.7	56	8.82	64	6.5	64	10.46	64	56.3	64	5.45	64	24.3
Top-cross 199	64	54.7	64	122.1	60	10.68	64	12.7	64	11.23	64	60.5	64	5.37	64	49.3
Top-cross 213	64	52.6	64	120.6	61	11.55	64	14.4	64	10.30	64	54.0	64	5.27	64	50.2
Top-cross 277	64	53.3	64	126.6	63	11.58	64	15.1	64	10.73	64	55.1	64	5.14	64	34.9
Top-cross 194	64	53.5	64	126.1	62	11.72	64	14.4	64	10.97	64	57.1	64	5.26	64	54.3
Top-cross 2D82-S5	64	55.3	63	122.4	64	12.82	64	12.6	64	10.99	64	54.4	64	4.98	64	49.7
Top-cross 100	64	55.8	63	117.0	63	10.34	64	13.0	64	10.58	64	51.8	64	4.96	64	44.5
Top-cross 106	64	54.2	63	123.3	64	12.31	64	14.3	64	11.08	64	56.5	64	5.17	64	47.8
Top-cross 195	64	53.0	64	127.0	58	9.92	64	16.6	64	10.24	64	55.8	64	5.48	64	48.5
Top-cross 220	64	53.6	64	123.5	63	11.26	64	15.3	64	11.09	64	58.1	64	5.29	64	50.3
Prolific	64	53.0	64	119.2	62	11.91	64	14.6	64	9.55	64	53.0	64	5.55	64	41.0

APPENDIX I. continued

Rye	Fertility		Grain/ Plant		Dry Weight/ Plant		Harvest Index		Kernel Weight		Straw Protein		Grain Protein	
Inbred 199	63	0.75	63	2.10	63	12.43	63	0.16	8	2.55	8	7.74	8	19.53
Inbred 213	64	0.43	64	1.48	64	7.97	64	0.17	8	2.25	8	6.05	8	18.98
Inbred 277	62	0.24	62	3.00	62	17.93	62	0.09	8	3.46	8	6.14	8	20.53
Inbred 194	64	0.65	64	4.11	64	17.36	64	0.21	8	3.16	8	5.83	8	20.54
Inbred 2D82-S5	64	0.60	64	2.47	64	9.26	64	0.26	8	3.60	8	6.23	8	18.49
Inbred 100	59	0.41	59	1.06	59	5.79	59	0.17	8	3.19	8	5.74	8	18.88
Inbred 106	63	0.43	63	1.73	63	8.17	63	0.19	8	2.86	8	7.31	8	15.89
Inbred 195	62	0.43	61	3.91	61	17.65	61	0.18	8	3.73	8	5.60	8	18.76
Inbred 220	64	0.42	64	2.94	64	13.19	64	0.19	8	3.68	8	7.21	8	18.35
Top-cross 199	64	0.82	64	13.74	64	41.38	64	0.32	8	5.13	8	5.76	8	17.19
Top-cross 213	64	0.92	64	14.04	64	42.53	64	0.32	8	4.96	8	5.24	8	17.58
Top-cross 277	64	0.63	64	14.00	64	47.10	64	0.29	8	6.35	8	5.09	8	18.88
Top-cross 194	64	0.95	64	17.72	64	49.15	64	0.35	8	5.30	8	4.44	8	18.36
Top-cross 2D82-S5	64	0.91	64	16.61	64	46.77	64	0.35	8	5.86	8	4.64	8	18.24
Top-cross 100	64	0.84	64	12.16	64	37.64	64	0.31	8	5.21	8	4.91	8	17.43
Top-cross 106	64	0.86	64	15.52	64	45.99	64	0.34	8	5.55	8	5.16	8	16.58
Top-cross 195	64	0.86	64	18.42	64	50.75	64	0.36	8	5.83	8	4.50	8	17.60
Top-cross 220	64	0.86	64	17.62	64	50.16	64	0.35	8	5.75	8	4.88	8	17.14
Prolific	64	0.77	64	14.05	64	42.58	64	0.33	8	5.70	8	5.50	8	18.25

APPENDIX II. Plant numbers and means for fifteen characters in the rye experiment grown in the growth cabinet

	Days to Heading				Plant Height (cm)				Flag Leaf Length (cm)				Spike Number			
	Rep. 1		Rep. 2		Rep. 1		Rep. 2		Rep. 1		Rep. 2		Rep. 1		Rep. 2	
Inbred 199	10	47.6	10	49.4	14	85.8	12	100.3	14	7.82	13	12.04	15	2.7	15	3.5
Inbred 213	15	46.7	15	48.3	15	104.1	15	92.1	15	8.10	15	7.13	15	3.3	15	4.5
Inbred 277	10	59.6	12	64.8	15	86.5	12	95.8	15	7.23	12	8.54	15	2.1	14	2.5
Inbred 194	15	49.9	14	50.9	15	109.5	15	93.3	15	11.53	15	10.60	15	3.7	15	3.4
Inbred 2D82-S5	15	44.1	15	44.1	15	100.3	15	90.0	15	8.40	15	11.40	15	3.7	15	3.7
Inbred 100	13	48.5	15	48.9	14	95.9	15	85.4	14	9.18	15	9.57	15	1.5	15	3.3
Inbred 106	15	44.1	14	43.7	15	105.2	14	93.9	15	12.07	14	14.32	15	3.6	14	3.4
Inbred 195	14	47.2	15	46.7	15	101.7	15	98.5	15	8.57	15	9.83	15	5.0	15	6.9
Inbred 220	10	49.5	14	52.1	13	89.7	14	82.6	12	8.21	14	9.18	13	1.5	14	3.1
Top-cross 199	13	47.6	15	46.7	15	120.9	15	122.3	15	11.83	15	10.87	15	4.2	15	6.3
Top-cross 213	15	41.7	15	41.8	15	123.5	15	123.7	15	9.77	15	11.30	15	5.8	15	8.7
Top-cross 277	12	44.0	14	43.6	13	124.4	14	127.4	13	10.27	14	13.61	14	4.4	15	7.3
Top-cross 194	15	44.3	15	43.3	15	129.1	15	116.7	15	12.50	15	12.20	15	4.7	15	7.4
Top-cross 2D82-S5	15	44.2	15	43.9	15	129.5	15	114.2	15	8.70	15	11.43	15	5.8	15	7.6
Top-cross 100	15	46.7	14	46.2	15	128.9	15	118.7	15	10.37	15	10.27	15	3.9	15	6.9
Top-cross 106	15	43.3	15	43.1	15	130.1	15	120.1	15	11.17	15	14.33	15	4.4	15	6.1
Top-cross 195	15	45.8	15	42.5	15	132.3	15	123.9	15	9.77	15	11.57	15	5.1	15	8.4
Top-cross 220	15	45.0	14	43.9	15	127.9	14	120.1	15	11.47	14	11.11	15	3.9	15	6.1
Prolific	15	40.3	15	40.2	15	127.8	15	118.7	15	12.20	15	13.37	15	5.4	15	7.9

APPENDIX II. continued

	Spike Length (cm)				Florets per Spike				Florets per cm				Kernels per Spike			
	Rep. 1		Rep. 2		Rep. 1		Rep. 2		Rep. 1		Rep. 2		Rep. 1		Rep. 2	
Inbred 199	14	8.54	15	8.90	14	58.3	15	60.8	14	6.74	15	6.84	14	17.6	15	22.0
Inbred 213	15	7.83	15	6.90	15	54.4	15	48.3	15	7.01	15	6.98	15	25.7	15	19.7
Inbred 277	13	5.81	14	6.11	13	37.2	14	34.1	13	6.53	14	5.59	13	7.2	14	7.0
Inbred 194	15	8.77	15	7.37	15	56.0	15	48.0	15	6.45	15	6.55	15	27.5	15	19.0
Inbred 2D82-S5	15	8.60	15	7.80	15	45.3	15	41.1	15	5.29	15	5.29	15	26.3	15	20.3
Inbred 100	13	6.85	15	7.07	13	43.7	15	45.3	13	6.37	15	6.45	13	11.7	15	10.0
Inbred 106	15	9.13	14	9.07	15	56.5	14	55.4	15	6.20	14	6.13	15	34.1	14	23.9
Inbred 195	14	8.04	15	7.03	14	52.0	15	47.2	14	6.54	15	6.72	14	18.8	15	12.5
Inbred 220	10	8.40	14	8.25	10	57.6	14	52.3	10	6.89	14	6.38	10	21.6	14	12.5
Top-cross 199	14	10.07	15	9.63	14	70.6	15	59.5	14	6.77	15	6.24	14	41.9	15	32.4
Top-cross 213	15	10.17	15	10.07	15	62.1	15	58.9	15	6.22	15	5.87	15	44.7	15	43.6
Top-cross 277	13	9.58	14	9.61	13	61.5	14	58.3	13	6.47	14	6.10	13	29.5	14	28.6
Top-cross 194	15	10.57	15	9.77	15	64.5	15	57.7	15	6.12	15	5.95	15	47.5	15	38.1
Top-cross 2D82-S5	15	10.13	15	9.60	15	60.0	15	51.5	15	6.03	15	5.36	15	43.7	15	36.3
Top-cross 100	15	9.30	15	9.47	15	53.1	15	54.7	15	5.77	15	5.81	15	34.6	15	34.1
Top-cross 106	15	10.17	15	10.50	15	62.4	15	62.1	15	6.19	15	5.97	15	43.4	15	41.4
Top-cross 195	15	9.50	15	9.57	15	59.7	15	57.6	15	6.38	15	6.03	15	43.4	15	37.9
Top-cross 220	15	10.57	14	10.14	15	65.3	14	60.3	15	6.33	14	5.98	15	42.1	14	34.6
Prolific	15	10.00	15	9.13	15	61.3	15	55.5	15	6.17	15	6.09	15	36.1	15	28.1

APPENDIX II. continued

	Fertility				Grain per Plant				Dry Weight per Plant				Harvest Index			
	Rep. 1		Rep. 2		Rep. 1		Rep. 2		Rep. 1		Rep. 2		Rep. 1		Rep. 2	
Inbred 199	14	0.33	15	0.37	15	0.57	15	0.73	15	3.43	15	3.64	15	0.14	15	0.16
Inbred 213	15	0.46	15	0.38	15	0.77	15	0.65	15	3.57	15	3.13	15	0.23	15	0.21
Inbred 277	13	0.17	14	0.20	15	0.39	14	0.24	15	2.77	15	2.21	15	0.07	14	0.10
Inbred 194	15	0.49	15	0.39	15	1.69	15	0.88	15	6.39	15	4.13	15	0.24	15	0.18
Inbred 2D82-S5	15	0.59	15	0.50	15	1.59	15	0.86	15	4.72	15	3.00	15	0.32	15	0.30
Inbred 100	13	0.28	15	0.22	15	0.27	15	0.39	15	2.00	15	2.69	15	0.13	15	0.14
Inbred 106	15	0.60	14	0.43	15	1.45	14	0.58	15	5.00	14	2.93	15	0.27	14	0.19
Inbred 195	14	0.38	15	0.26	15	1.23	15	0.89	15	5.93	15	5.23	15	0.19	15	0.15
Inbred 220	10	0.36	14	0.23	13	0.85	14	0.58	13	3.48	15	3.29	13	0.17	14	0.14
Top-cross 199	14	0.60	15	0.55	14	3.47	15	3.48	15	11.07	15	9.71	14	0.30	15	0.35
Top-cross 213	15	0.72	15	0.74	15	4.83	15	5.01	15	12.39	15	12.43	15	0.39	15	0.41
Top-cross 277	13	0.49	14	0.49	13	3.32	14	3.99	14	9.28	15	11.61	14	0.31	14	0.34
Top-cross 194	15	0.73	15	0.67	15	5.01	15	4.54	15	12.24	15	11.26	15	0.41	15	0.40
Top-cross 2D82-S5	15	0.73	15	0.71	15	5.84	15	4.93	15	14.41	15	12.12	15	0.41	15	0.39
Top-cross 100	15	0.66	15	0.62	15	3.09	15	3.79	15	9.13	15	9.45	15	0.34	15	0.41
Top-cross 106	15	0.70	15	0.67	15	4.21	15	3.49	15	11.27	15	9.23	15	0.38	15	0.37
Top-cross 195	15	0.72	15	0.67	15	4.64	15	5.05	15	12.72	15	12.19	15	0.38	15	0.41
Top-cross 220	15	0.65	14	0.57	15	3.77	14	3.41	15	11.37	15	9.58	15	0.33	14	0.33
Prolific	15	0.59	15	0.51	15	4.55	15	3.85	15	13.17	15	10.99	15	0.35	15	0.35

APPENDIX II. continued

	Kernel Weight				Straw Protein				Grain Protein			
	Rep. 1		Rep. 2		Rep. 1		Rep. 2		Rep. 1		Rep. 2	
Inbred 199	3	2.97	3	2.60	3	11.83	3	9.73	3	18.67	3	16.87
Inbred 213	3	2.57	3	2.00	3	8.40	3	8.50	3	14.97	3	16.53
Inbred 277	3	4.23	3	2.47	3	10.87	3	9.27	2	18.75	2	21.00
Inbred 194	3	4.10	3	3.10	3	8.27	3	8.53	3	19.77	3	20.90
Inbred 2D82-S5	3	4.73	3	3.60	3	6.43	3	6.70	3	17.50	3	18.00
Inbred 100	3	4.30	3	3.50	3	9.93	3	8.67	3	18.30	3	20.20
Inbred 106	3	3.33	3	2.57	3	7.07	3	8.07	3	16.10	3	18.97
Inbred 195	3	4.20	3	3.23	3	8.87	3	8.43	3	18.47	3	20.67
Inbred 220	3	5.40	3	3.37	3	9.27	3	8.93	3	15.47	3	18.27
Top-cross 199	3	5.03	3	4.83	3	9.57	3	7.13	3	17.53	3	16.43
Top-cross 213	3	5.46	3	4.57	3	6.90	3	6.57	3	15.00	3	14.13
Top-cross 277	3	7.17	3	5.77	3	8.63	3	6.10	3	17.00	3	16.87
Top-cross 194	3	6.00	3	5.17	3	5.60	3	5.13	3	15.77	3	15.87
Top-cross 2D82-S5	3	6.57	3	5.30	3	5.37	3	5.63	3	15.70	3	16.20
Top-cross 100	3	5.90	3	5.40	3	7.10	3	5.73	3	16.33	3	15.27
Top-cross 106	3	5.60	3	4.53	3	7.03	3	5.53	3	15.30	3	15.33
Top-cross 195	3	6.07	3	5.17	3	6.77	3	4.67	3	17.10	3	15.63
Top-cross 220	3	6.53	3	4.90	3	7.47	3	6.10	3	15.53	3	16.20
Prolific	3	6.83	3	5.83	3	6.37	3	5.83	3	16.23	3	17.77

APPENDIX III. Plant numbers and means for fifteen characters of twenty-one lines of hexaploid triticales

Cross	C1 Plant	Days to Heading	Plant Height(cm)	Flag Leaf Length(cm)	Spike Number	Spike Length(cm)	Florets/ Spike	Florets/ cm
Jori X Snoopy	18	14 53.6	14 94.4	14 21.29	14 3.3	14 10.61	14 58.1	14 5.48
Jori X Snoopy	19	14 47.6	14 105.8	14 22.75	14 3.4	14 11.21	14 61.9	14 5.54
Jori X Snoopy	15	14 49.3	14 96.2	14 24.11	14 5.5	14 11.25	14 62.4	14 5.56
Jori X Snoopy	17	14 49.0	14 101.7	14 23.89	14 5.4	14 11.04	14 60.4	14 5.50
Jori X Snoopy	22	14 49.1	14 101.1	14 26.32	14 3.8	14 11.89	14 61.5	14 5.19
Jori X Inbred 213	578	11 56.2	12 59.9	12 20.96	13 1.6	12 7.58	12 48.8	12 6.58
Jori X Inbred 213	550	13 62.5	13 86.4	13 21.92	13 1.3	13 8.19	13 50.5	13 6.21
Jori X Inbred 213	658	14 64.9	14 99.3	14 19.89	14 1.4	14 8.57	14 51.4	14 6.01
Jori X Inbred 213	397	12 62.4	13 82.3	13 19.92	13 1.2	12 8.42	12 55.3	12 6.58
Jori X Inbred 220	253	14 58.5	14 99.3	14 20.93	14 2.7	14 11.75	14 70.9	14 6.06
Jori X Inbred 220	587	14 54.7	14 100.4	14 21.39	14 2.5	14 10.86	14 68.6	14 6.34
Jori X Inbred 220	537	14 53.1	14 102.1	14 22.79	14 3.5	14 12.75	14 78.4	14 6.19
Jori X Inbred 220	81	14 51.8	14 98.9	14 21.04	14 2.9	14 11.64	14 69.6	14 6.01
Jori X Inbred 194	585	14 48.7	14 101.9	14 25.11	14 4.3	14 10.79	14 64.7	14 6.00
Jori X Inbred 194	584	14 50.1	14 107.5	14 25.46	14 3.8	14 10.89	14 65.4	14 6.02
Jori X Inbred 194	654	14 51.7	14 101.1	14 25.46	14 2.7	14 9.79	14 65.6	14 6.72
Jori X Inbred 100	623	14 64.7	14 97.7	14 22.71	14 1.3	14 8.11	14 54.9	14 6.90
Jori X Inbred 100	625	13 64.2	13 101.0	14 19.36	14 1.3	13 8.54	13 56.5	13 6.67
Jori X Inbred 106	610	14 59.0	14 100.1	14 21.68	14 1.6	14 9.46	14 61.7	14 6.53
Jori X Inbred 106	168	13 55.4	13 97.6	13 23.81	13 1.3	13 9.50	13 56.3	13 5.98
Jori X Inbred 277	556	14 57.5	14 113.7	14 19.93	14 3.1	14 11.46	14 61.7	14 5.41

APPENDIX III. continued

C1 Plant	Kernels/ Spike		Fertility		Grain/ Plant		Dry Weight/ Plant		Harvest Index		Kernel Weight		Straw Protein		Grain Protein	
18	14	17.7	14	0.30	14	1.96	14	9.61	14	0.20	2	12.95	2	7.90	2	23.60
19	14	33.1	14	0.53	14	3.99	14	10.73	14	0.36	2	10.00	2	6.60	2	19.00
15	14	29.6	14	0.47	14	5.29	14	15.72	14	0.33	2	14.00	2	6.95	2	20.00
17	14	16.3	14	0.27	14	3.19	14	14.27	14	0.21	2	13.35	2	7.70	2	23.10
22	14	42.6	14	0.69	14	7.44	14	15.97	14	0.46	2	11.65	2	6.00	2	18.25
578	12	7.2	12	0.13	12	0.40	13	2.34	12	0.11	2	8.05	2	11.85	2	21.55
550	13	9.6	13	0.18	13	0.45	14	2.01	13	0.20	2	8.05	2	9.50	2	20.10
658	14	10.2	14	0.19	14	0.49	14	2.55	14	0.18	2	8.05	2	8.80	2	19.40
397	12	10.1	12	0.18	12	0.63	13	2.23	12	0.25	2	8.60	2	9.90	2	19.20
253	14	7.4	14	0.10	14	0.47	14	12.84	14	0.03	2	9.15	2	10.65	2	20.10
587	14	18.6	14	0.27	14	2.12	14	10.25	14	0.18	2	12.05	2	10.55	2	19.40
537	14	9.1	14	0.12	14	1.06	14	13.80	14	0.10	2	13.40	2	11.35	2	21.25
81	14	9.1	14	0.13	14	0.73	14	10.91	14	0.05	2	10.65	2	9.85	2	20.40
585	14	16.7	14	0.26	14	2.87	14	13.07	14	0.21	2	12.15	2	9.15	2	20.95
584	14	10.2	14	0.16	14	1.44	14	13.08	14	0.10	2	12.50	2	9.05	2	23.00
654	14	31.8	14	0.48	14	3.14	14	9.35	14	0.33	2	11.35	2	7.65	2	19.45
623	14	6.1	14	0.10	14	0.42	14	3.26	14	0.09	2	10.00	2	9.25	2	19.45
625	13	9.3	13	0.15	13	0.54	14	3.35	13	0.14	2	9.45	2	9.60	2	18.30
610	14	20.4	14	0.32	14	1.29	14	4.16	14	0.28	2	9.70	2	7.50	2	17.00
168	13	19.8	13	0.34	13	1.45	13	3.98	13	0.34	2	10.15	2	7.55	2	16.35
556	14	5.2	14	0.09	14	0.66	14	11.21	14	0.06	2	9.10	2	10.00	2	23.10

APPENDIX IV. Means for fifteen characters of twenty-seven lines of octoploid triticale

Cross	C1 Plant	Days to Heading*	Plant Height(cm)*	Flag Leaf Length(cm)*	Spike Number*	Spike Length(cm)*	Florets/ Spike*	Florets/ cm*
Sonora 64 X Inbred 199	179	53.0	80.7	15.10	2.4	11.45	70.2	6.21
Sonora 64 X Inbred 199	181	56.5	85.3	13.90	2.1	12.45	66.3	5.34
Sonora 64 X Inbred 199	218	46.9	81.5	16.05	2.8	12.25	61.8	5.06
Sonora 64 X Inbred 199	221	49.2	86.9	17.75	5.0	13.85	69.3	5.06
Sonora 64 X Inbred 199	225	51.4	95.3	17.50	3.6	14.15	70.2	5.05
Sonora 64 X Inbred 199	230	51.7	85.7	14.50	1.9	17.70	63.3	5.47
Sonora 64 X Inbred 199	278	60.3	98.4	14.45	1.9	11.60	64.8	5.59
Sonora 64 X Inbred 2D82-S5	90	49.3	80.3	15.20	3.8	10.10	65.4	6.53
Sonora 64 X Inbred 2D82-S5	94	49.2	77.3	13.10	3.7	9.65	60.6	6.35
Sonora 64 X Inbred 2D82-S5	114	43.8	79.4	16.40	4.8	10.55	59.7	5.71
Sonora 64 X Inbred 2D82-S5	115	52.4	60.0	12.75	2.3	7.85	57.3	7.32
Sonora 64 X Inbred 2D82-S5	125	45.7	71.8	17.85	6.0	10.40	61.2	5.94
Sonora 64 X Inbred 2D82-S5	194	44.6	75.1	17.80	4.8	10.75	64.2	6.01
Sonora 64 X Inbred 194	264	50.7	77.5	14.45	3.7	9.05	60.6	6.77
Sonora 64 X Inbred 194	265	47.1	87.3	17.60	3.0	12.60	64.2	5.11
Sonora 64 X Inbred 194	309	45.4	69.9	20.95	2.7	10.80	47.7	4.45
Sonora 64 X Inbred 194	323	44.7	70.2	17.90	5.2	10.85	56.1	5.26
Sonora 64 X Inbred 194	324	49.6	76.8	14.55	3.1	12.35	66.6	5.42
Sonora 64 X Snoopy	46	54.8	75.9	14.65	3.4	12.30	72.9	5.97
Sonora 64 X Snoopy	48	52.4	76.6	13.55	3.3	9.55	59.4	6.33
Sonora 64 X Snoopy	52	52.0	76.0	15.40	3.4	11.50	66.0	5.76
Sonora 64 X Snoopy	57	45.9	65.2	19.00	2.7	10.70	48.9	4.66
Sonora 64 X Snoopy	66	58.6	73.4	15.40	2.2	10.10	64.8	6.45
Sonora 64 X Inbred 220	107	49.7	74.5	16.30	3.7	11.90	65.1	5.51
Sonora 64 X Inbred 220	82	50.1	70.0	16.40	3.7	11.70	54.9	4.74
Sonora 64 X Inbred 220	108a	54.1	83.1	14.60	2.9	11.80	71.7	5.42
Sonora 64 X Inbred 220	108b	50.6	70.7	17.60	3.1	10.80	63.0	5.99

* each value is a mean of ten plants

APPENDIX IV. continued

Cl Plant	Kernels/ Spike*	Fertility*	Grain/ Plant*	Dry Weight/ Plant*	Harvest Index*	Kernel Weight**	Straw Protein**	Grain Protein**
179	11.2	0.16	0.60	7.10	0.07	7.08	11.71	23.16
181	4.5	0.07	0.13	4.85	0.02	5.58	11.72	23.35
218	2.4	0.04	0.11	6.08	0.02	8.69	10.90	23.86
221	9.9	0.14	0.72	10.93	0.07	8.27	11.67	25.05
225	5.6	0.08	0.40	9.77	0.03	8.48	11.54	25.42
230	2.7	0.04	0.14	5.29	0.03	7.43	12.36	22.60
278	4.8	0.07	0.17	6.43	0.03	4.89	11.77	24.69
90	0.7	0.01	0.03	8.26	0.01	5.84	12.32	-----
94	0.8	0.01	0.06	6.97	0.01	9.00	11.81	-----
114	9.3	0.15	0.84	9.83	0.08	8.20	10.58	23.06
115	1.0	0.02	0.07	3.98	0.04	5.45	12.96	-----
125	0.03	0.01	0.02	9.10	0.01	6.67	10.86	-----
194	12.9	0.20	1.13	9.23	0.11	8.28	10.22	22.88
264	11.4	0.18	0.82	8.34	0.08	5.76	11.49	25.61
265	11.8	0.18	1.04	10.31	0.09	8.24	10.72	22.83
309	5.9	0.13	0.37	5.49	0.06	6.63	10.54	25.82
323	5.0	0.09	0.37	6.39	0.05	5.99	12.27	24.11
324	21.3	0.32	1.34	6.63	0.20	8.49	10.08	19.06
46	3.8	0.05	0.31	7.66	0.04	6.35	11.40	24.22
48	1.7	0.03	0.12	6.82	0.02	6.94	12.35	21.79
52	0.7	0.01	0.04	7.61	0.01	6.67	11.58	-----
57	8.2	0.16	0.30	3.64	0.08	4.15	11.90	26.18
66	1.0	0.02	0.11	4.06	0.02	4.00	12.68	26.34
107	5.3	0.08	0.24	7.78	0.03	6.97	11.17	23.29
82	2.3	0.04	0.09	4.67	0.02	4.39	11.45	22.08
108a	8.1	0.11	0.68	7.64	0.07	10.29	10.85	19.80
108b	8.7	0.14	0.41	7.69	0.06	7.04	12.23	23.55

* each value is a mean of ten plants

** each value is a mean of two samples

APPENDIX V. Plant numbers and means of Snoopy, inbred 2D82-S5, and top-cross 194 rye lines grown in the growth cabinet.

	Snoopy		Inbred 2D82-S5		Top-cross 194	
Days to Heading	29	49.9	11	43.8	11	42.5
Plant Height	29	102.0	12	95.4	11	119.7
Flag Leaf Length	29	9.79	12	9.04	11	10.50
Spike Number	29	5.7	12	4.0	11	6.6
Spike Length	29	8.21	12	8.04	11	10.18
Florets per Spike	29	55.7	12	38.5	11	56.7
Florets per cm	29	6.76	12	4.79	11	5.61
Kernels per Spike	29	20.9	12	21.3	11	37.5
Fertility	29	0.37	12	0.57	11	0.66
Grain per Plant	29	1.85	12	1.35	11	4.98
Dry Weight per Plant	29	7.48	12	4.73	11	11.90
Harvest Index	29	0.23	12	0.30	11	0.66
Kernel Weight	6	5.40	2	4.95	2	6.35
Straw Protein	6	10.25	2	8.45	2	8.85
Grain Protein	6	16.86	2	16.65	2	15.60