

THE UNIVERSITY OF MANITOBA

A STUDY OF THE POTENTIAL OF HYBRID RYE (*Secale cereale* L.)

PRODUCED BY CROSSES BETWEEN INBRED LINES.

by

GRAHAM JOHN SCOLES

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF PLANT SCIENCE

WINNIPEG, MANITOBA

October, 1975

**"STUDY OF THE POTENTIAL OF HYBRID RYE (SECALE CEREALE L.)  
PRODUCED BY CROSSES BETWEEN INBRED LINES"**

by

**GRAHAM JOHN SCOLES**

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

**MASTER OF SCIENCE**

**© 1975**

**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.**

## ACKNOWLEDGEMENTS

The author wishes to express his sincere gratitude to Dr.L.E.Evans for offering him the opportunity to carry out this project under his supervision, and also to express his appreciation of the guidance and comments afforded him during the course of the project.

The author also wishes to extend his sincere appreciation to those that assisted him during the project; to Mr.D.Zuzens for useful discussion,suggestions,and technical assistance;to Dr.R.J.Baker for his help with the analysis of the results and his patience during discussions on their interpretation;also to the students of Plant Science that assisted during seeding and harvesting.

Financial assistance from the University of Manitoba is also gratefully acknowledged.

Finally the author wishes to express his gratitude to Dr.P.J.Kaltsikes for initially bringing him to Winnipeg, where many good things have begun.



ABSTRACTA STUDY OF THE POTENTIAL OF HYBRID RYE PRODUCED  
BY CROSSES BETWEEN INBRED LINES.

by

GRAHAM J. SCOLES

DEPARTMENT OF PLANT SCIENCE

UNIVERSITY OF MANITOBA.

Thirteen rye hybrids were produced by making thirteen crosses between eleven different, unselected inbred lines which had been inbred for at least four generations. Two experiments were performed using this material. In the first, the hybrids and inbreds together with some outbreeding rye varieties and some wheat and triticale lines were grown in the field. During the growing season a total of eleven different characters of the material were evaluated. In the second experiment some hybrids and inbreds were grown in a controlled environment cabinet and early growth characteristics of the lines were evaluated up to 38 days after seeding.

Hybrids initially had smaller seed than the inbreds. This was attributed to the crossing technique used in producing the hybrid seed. However, this factor did not affect the early growth of the hybrids as in the field, emergence was significantly better than that of the inbreds. Hybrids were also superior to the inbreds in their early growth as measured in the controlled environment cabinet. Hybrids were significantly different from the inbreds in all other characters. They headed earlier, had more tillers per plant, were taller, and had more florets per head. The

hybrids also had significantly higher cross and self-fertility than the inbreds under field conditions, yielded significantly more and had a significantly higher one hundred kernel weight than the inbreds.

When compared to the control variety Gazelle the hybrids as a group were similar in many respects although individual lines differed from Gazelle. The hybrids were not significantly different from Gazelle in either emergence, days to heading, head size or the level of fertility. As expected the outbred varieties were very self-sterile, whereas the hybrids had high self-fertility. The hybrids also had significantly more tillers per plant than Gazelle and were significantly taller. Although the hybrids as a group had significantly lower yield than Gazelle and smaller one hundred kernel weight, certain hybrids were superior to Gazelle.

It was concluded that with suitable selection of inbred lines, hybrids could be obtained which were superior to the current outbred varieties. Further tests would be required to determine the full potential of hybrid rye and its economic feasibility.

## LIST OF FIGURES AND TABLES

		<u>Page</u>
Figure 1.	Production of rye in the major producing areas over the period 1924-1974.	6
Figure 2.	Area of rye in the major producing areas over the period 1924-1974.	7
Figure 3.	Average yields of rye in the major producing areas over the period 1924-1974.	8
Table 1.	Utilization of rye in selected countries, averages 1955/56-1958/59 and 1959/60-1962/63.	10
Table 2.	Differences between rye and wheat (rye-wheat) in the levels of nine amino-acids as reported from three different sources.	16
Table 3.	Metabolizable energy values of rye, wheat, barley, oats and corn when fed to four different species.	18
Table 4.	The origin and seed-type of the twelve inbred lines chosen as parents.	42
Table 5.	Characteristics of the twelve inbred lines when grown in the glasshouse.	48
Table 6.	Values of eleven characters of the eleven inbred lines when grown in the field as part of the first experiment.	49
Table 7.	Values of eleven characters of the thirteen hybrid lines when grown in the field as part of the first experiment.	57

	<u>Page</u>
Table 8.	Values of eleven characters of the controls used in the first experiment together with mean values for hybrids and inbreds and an L.S.D. for comparison of any two lines. 58
Table 9.	Correlation coefficients between hybrids and their parents for various characters. 61
Table 10.	Measurements taken over a period of 38 days on inbreds and hybrids grown in a controlled environment, with F-values from the analysis of variance of the two groups. 63
Table 11	The yield of certain hybrid lines in relation to the yield of their parents. 75

## LIST OF APPENDIX TABLES

	<u>Page</u>
Appendix I. Analysis of variance tables for the eleven characters analysed in the first experiment.	89
Appendix II. Correlation coefficients between characters among the inbred and hybrid lines.	92



## TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGEMENTS .....	ii
ABSTRACT .....	iii
LIST OF FIGURES AND TABLES .....	v
LIST OF APPENDIX TABLES .....	vii
1. INTRODUCTION .....	1
2. LITERATURE REVIEW	
2.1 The Origin and Domestication of Rye .....	3
2.2 The History of World Rye Production and Consumption .....	5
2.3 Rye as an Animal Feed .....	11
2.3A The presence of toxic substances in the rye kernel .....	12
2.3B The nutritive quality of rye .....	15
2.4 The Future of Rye .....	20
2.5 Heterosis in Rye .....	22
2.5A Heterosis between varieties .....	23
2.5B Heterosis between inbreds .....	29
2.6 The Genetic and Physiological Basis of Heterosis .....	34
2.7 Estimating Levels of Heterosis .....	37
2.8 Cytoplasmic Male-Sterility in Rye .....	39
3. MATERIALS AND METHODS	
3.1 The Production of Hybrids and Multiplication of Inbreds .....	41
3.2 Yield Testing the Hybrids .....	44

	<u>Page</u>
3.3 The Early Growth of Inbreds and Hybrids .....	46
4. RESULTS AND DISCUSSION	
4.1 Characteristics of the Inbred Lines .....	47
4.2 Comparison of Inbreds, Hybrids and Out- Pollinated Control Varieties .....	56
5. CONCLUSIONS AND RECCOMENDATIONS .....	77
LITERATURE CITED .....	79
APPENDIX .....	88

## 1. INTRODUCTION

In Western Canada in 1974 rye occupied only 340,000 hectares, just 1.8% of the 18.9 million hectares sown to the four major small-grain cereals (wheat, barley, oats and rye). Traditionally rye has never been held in high esteem as either a bread grain, because of the heavy dark loaf it produces (Horsley 1969), or as an animal feed, because of the low palatability and growth inhibiting factors associated with high levels of rye in a ration (F.A.O. 1965). Due to this reputation world demand for rye has decreased whereas demand for the other cereals continues to increase. As a result world prices for rye have been lower and profits to the farmer less than for other small-grains (F.A.O. 1965). Nevertheless, rye has advantages over the other cereals with respect to winter-hardiness and its ability to grow on sandy or infertile soils which cannot sustain the other cereals (Reeves 1971). With adequate fertilization, rye yields equal to wheat are attainable and its quality with respect to protein and amino-acid balance is generally recognized as being as good as or better than that of wheat (Canada Grains Council 1974).

There is now a growing awareness in Western Canada of the potential of rye as "the preferred grain crop for extensive areas, especially for rotation purposes with other cereals" (Canada Grains Council 1970). If problems of palatability and growth inhibition can be determined and overcome an increase in demand for rye as an animal feed might be expected. It would seem desirable to have some improved, adapted, high-yielding rye varieties available. In the past a minimum of effort has been afforded rye by Canadian plant-breeders, many of the varieties

being based on selections from introduced varieties. There is now interest in attempting to improve rye using some of the established methods of breeding cross-pollinated crops. One possible breeding technique would be to utilize heterosis in rye and produce hybrid varieties. Virtually 100% of the corn now grown in North America is hybrid corn produced by controlled crossing of inbred-lines. Rye, like corn, is a naturally outbreeding plant and similar inbred lines have been produced and maintained. With the recent discovery and release of a source of cytoplasmic male-sterility in rye (Geiger and Schnell 1970), the mechanics of producing an  $F_1$  rye hybrid are relatively simple and the prospect of a hybrid rye variety seems much closer. This study was undertaken in an attempt to ascertain the feasibility of hybrid rye production by obtaining some measure of the level of heterosis expressed in  $F_1$  rye hybrids produced by crossing inbred lines.

## 2. LITERATURE REVIEW

### 2.1 The Origin and Domestication of Rye

Cultivated rye, *Secale cereale* L. is classified as belonging to the tribe *Triticeae* of the family *Gramineae*. The genus *Secale* contains only four to twelve species (depending on the criteria used) most of which have been suggested as the immediate ancestor of cultivated rye by various authors (Stutz 1972). Stutz has recently proposed that cultivated rye originated from weedy products derived from the introgression of *S. montanum* Guss. into *S. vavilovii* Grossh., *S. vavilovii* itself having been derived from *S. silvestre* Host. *S. silvestre* in turn was thought to have been derived from *S. montanum* or a common ancestor. As *S. vavilovii* evolved from *S. montanum* via *S. silvestre* an evolutionary series of stepwise translocations occurred which have recently been identified by van Heemert and Sybenga (1972).

The early forms of cultivated rye are thought to have evolved after the period 7,000 B.C. that is now estimated for the origin of wheat and barley (Horsley 1969). The first weedy forms of rye are believed to have evolved in central Asia about 6,000 years ago (Helbaek 1971). Unlike wheat and barley which were domesticated in the immediate area of their centre of origin, and then spread as a crop, Helbaek has suggested that rye was introduced into Europe via the Balkan peninsula as a weed of other cereals. He further proposes that nomads were responsible for the original introduction, and rye then became distributed throughout Europe and into Russia by armies and other travelling people. Its dissemination as a weed was originally aided by the presence of rough awns and a fragile rachis (Helbaek 1971). Domestication of rye

is thought to have taken place at several independent locations (Khush 1963). As it was carried as a weed into higher altitudes and more Northerly latitudes its competitive ability relative to wheat and barley increased, and eventually rye became the dominant component of the crop (Helbaek 1971). As domestication proceeded unconscious selection favoured a stiff, non-shattering rachis, and winnowing favoured a larger grain (Khush 1963). As a result, rye became the primary bread-grain of much of Eastern Europe, Russia, Germany, the low countries and Scandinavia until the 17th century and was brought across to the New World as an important staple of the Founding Fathers (Horsley 1969).

## 2.2 The History of World Rye Production and Consumption

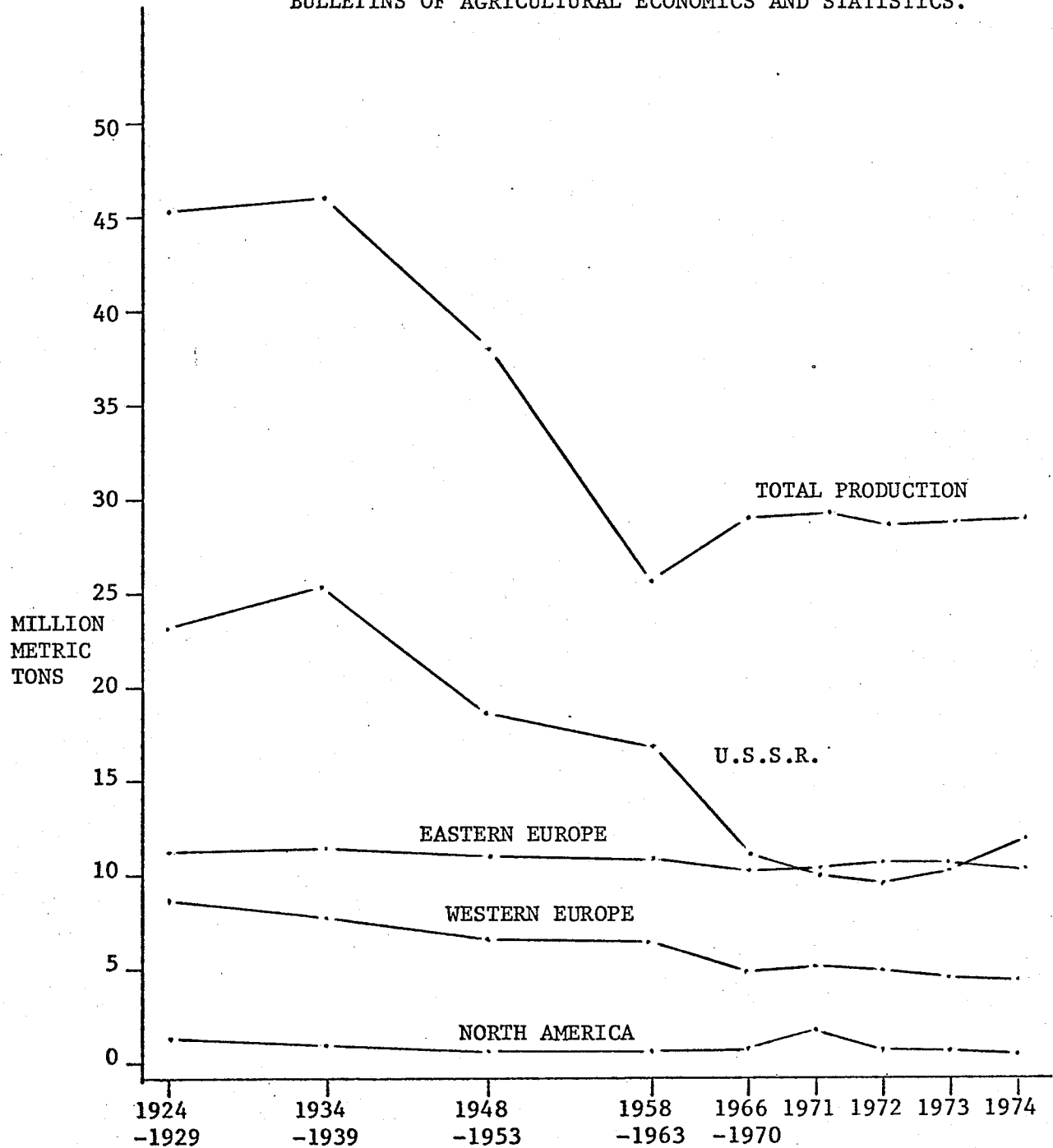
Once the most common bread grain in much of Europe and Russia, the importance of rye as a major cereal has declined steadily since the seventeenth century (Horsley 1969). By 1918, world wheat production had increased to a level double that of rye. In the last half-century production of wheat has more than tripled, whereas rye production reached a peak in the pre-war period 1934-39 and has since declined to the level of the early twentieth century. However, in recent years production seems to have stabilized at around 30 million metric tons (Figure 1) less than 10% of the 1974 world wheat production. In the last forty years decreases in production of rye have been paralleled by similar decreases in the acreage grown in major producing areas (Russia, Eastern Europe, Western Europe and North America) (Figure 2) but these have been partly offset by consistent increases in yield obtained through the use of better varieties and improved cultural practices (Figure 3).

Changes in food preference have been largely responsible for the decline in popularity of rye as a bread-grain, especially in Teutonic and Slavic nations where rye has been the traditional bread (Horsley 1969). Also, increased affluence in industrial Europe allowed the switch to the more expensive wheat bread as people clung to the ancient belief that the dark, compact rye bread was an inferior product (Horsley 1969). As incomes increased further, and wheat bread became less expensive because of new wheat varieties and improved technology, wheat was able to oust rye as the dominant food grain (Schaben 1948). This trend seems irreversible and has continued up to the present day in both Russia and Eastern Europe. Poland is now the only country where rye production is greater than wheat but if trends continue, by 1976 wheat

FIGURE I. PRODUCTION OF RYE IN THE MAJOR PRODUCING AREAS

OVER THE PERIOD 1924-1974. SOURCE: F.A.O. MONTHLY

BULLETINS OF AGRICULTURAL ECONOMICS AND STATISTICS.





**FIGURE 2. AREA OF RYE GROWN FOR GRAIN IN THE MAJOR PRODUCING AREAS OVER THE PERIOD 1924-1974. SOURCE: F.A.O. MONTHLY BULLETINS OF AGRICULTURAL ECONOMICS AND STATISTICS.**

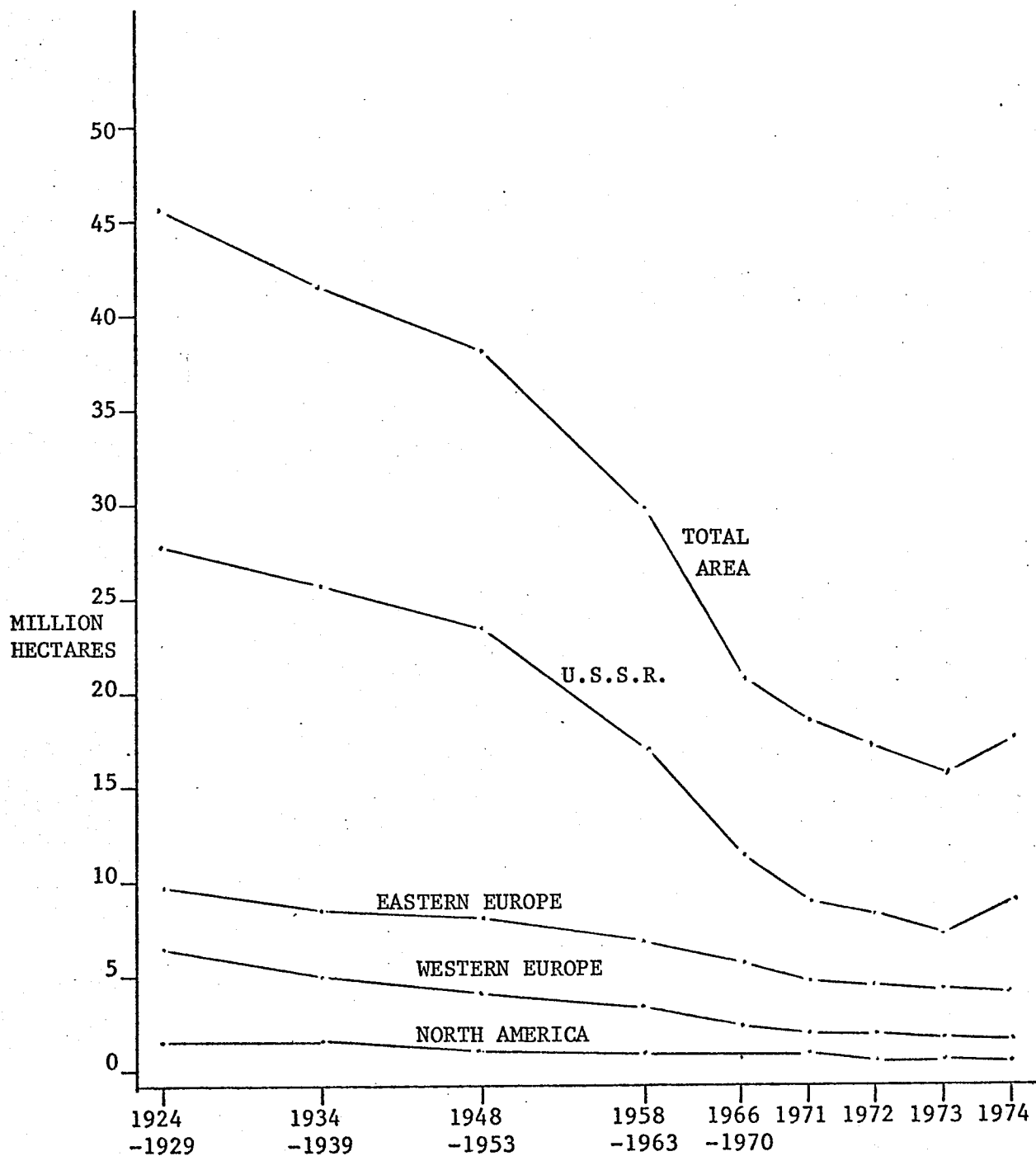
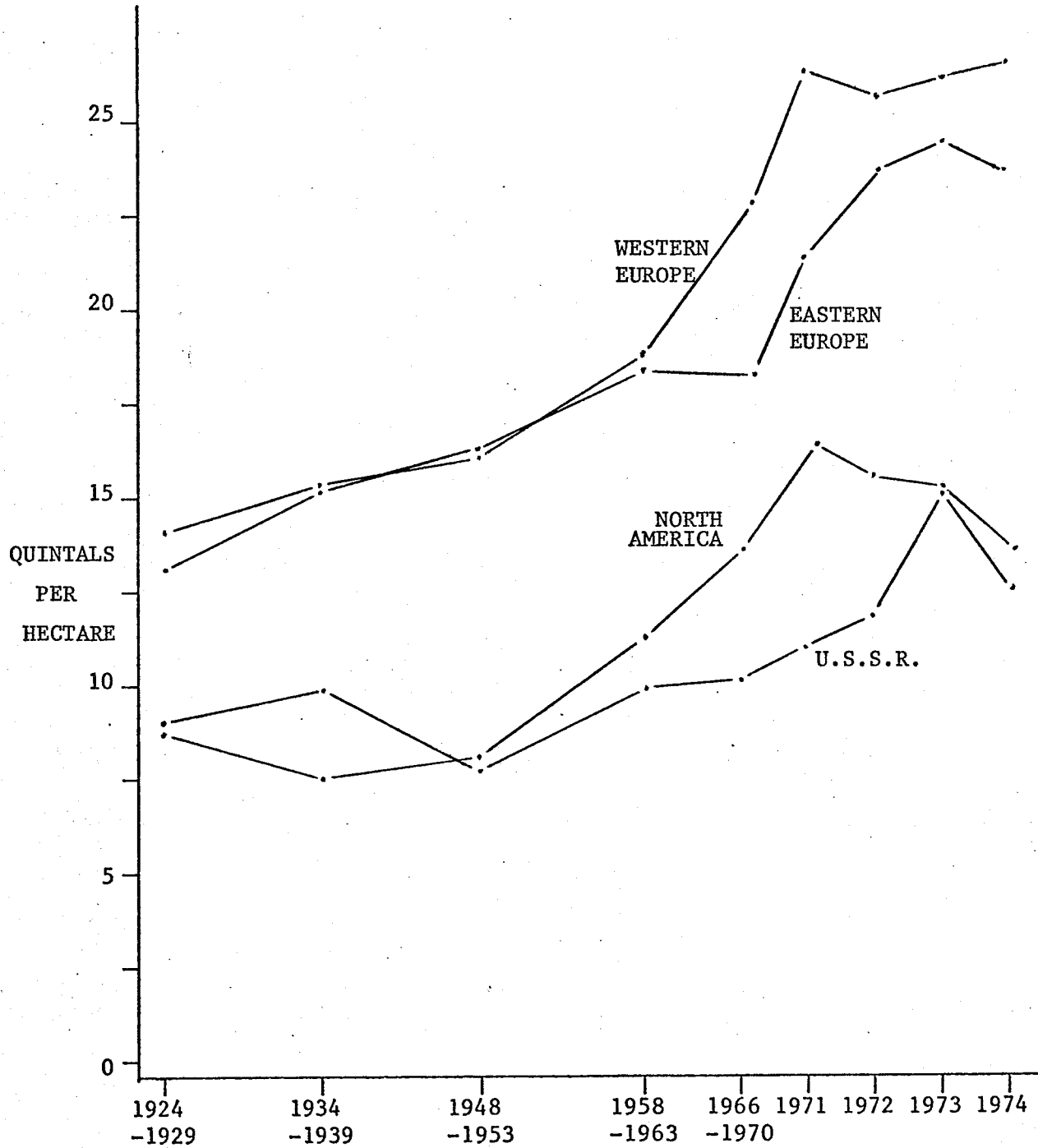


FIGURE 3. AVERAGE YIELDS OF RYE IN THE MAJOR PRODUCING

AREAS OVER THE PERIOD 1924-1974. SOURCE: F.A.O.

MONTHLY BULLETINS OF AGRICULTURAL ECONOMICS AND STATISTICS.



production will have increased above that of rye. However, it seems unlikely that traditional preferences for rye-bread in these areas will die out immediately (F.A.O. 1965).

In recent years the decline in consumption of rye in the form of bread has been partly offset by an increase in the use of rye as a feed grain. World figures for trends in rye consumption are not readily available, but figures obtained by the F.A.O. (Table 1) which exclude the centrally planned countries, the major areas of rye production and consumption, show that over the period 1955-1963 utilization of rye as a food declined from 4.0 to 3.5 million tons, whereas utilization as animal feed increased from 3.8 to 4.4 million tons. In Canada up to 1969 there had been only a slight increase in the use of rye for animal feed, 3,698 thousand bushels compared to 3,633 thousand in 1957. Over the same period human consumption of rye also increased from 429 to 450 thousand bushels (Carmichael and Norman 1970). In the U.S.A. human consumption of rye decreased from 5.2 million bushels in 1950 to 4.5 million bushels in 1960 and had returned to 1950 levels by 1970. Over the same period consumption as feed increased from 5.4 million bushels to 10.0 million bushels in 1960 and to 13.0 million bushels in 1970 (U.S.D.A. 1971). Because of this change in consumption patterns, rye, although like wheat a gluten containing grain (allowing it to be used in bread-making) is now regarded by bodies such as the F.A.O. as a feed or coarse grain rather than a bread grain.

TABLE 1. UTILIZATION OF RYE IN SELECTED COUNTRIES, AVERAGES<sup>1</sup> 1955/56-1958/59 AND 1959/60-1962/63 (THOUSAND METRIC TONS).

COUNTRY OR AREA	USE	
	FEED	FOOD
EUROPE AND SCANDINAVIA		
1955-1959	3,006	3,481
1959-1963	3,530	2,882
NORTH AMERICA		
1955-1959	321	131
1959-1963	307	127
ARGENTINA		
1955-1959	348	-
1959-1963	509	-
OTHERS		
1955-1959	110	406
1959-1963	70	481
TOTAL		
1955-1959	3,821	4,018
1959-1963	4,416	3,490

<sup>1</sup>(F.A.O. 1965).

### 2.3 Rye as an Animal Feed

It is unlikely that the recent rise in the feed uses of rye signifies a growing preference for rye in livestock feeding, but rather reflects its price advantage over other cereals as demand for rye has decreased (F.A.O. 1965). However, the future of rye as a crop in Canada will depend largely on an increase in its use as an animal feed. The previous limited use of rye in livestock feeding has been ascribed to the relatively low feed value of rye, and to the farmers traditional preferences for other grains (F.A.O. 1965), unwarranted prejudice against rye as a bread grain may have affected its popularity as a feed grain (Horsley 1969). Rye may also have been discredited as a feed because of its susceptibility to the disease ergot (*Claviceps purpurea* L.) which can be toxic to animals and may have contaminated early feed samples.

Knierem (1900) reported negative effects of feeding rye rather than barley after tests on a variety of animals. Crampton (1936) reviewed the literature on feed grains and concluded that of the five grains wheat, oats, barley, corn and rye; rye was inferior in its ability to sustain growth. Problems of feeding rye now seem to fall into three distinct areas; firstly, inclusion of rye in a diet has been found to affect palatability adversely resulting in decreased feed uptake. Secondly, high levels of rye in a diet have caused decreases in growth rates without a decrease in food uptake. And thirdly, rye has been found to induce various digestive disturbances in livestock, especially poultry. Problems of palatability, digestive disturbances and decreased growth rates have been associated with toxic substances present in the rye kernel and a number of experiments have been performed

in an attempt to ascertain safe levels of rye in a diet and to identify these factors. The decreased growth rates of livestock fed diets containing high levels of rye have also been ascribed to the low nutritional value of the cereal *per se*.

### 2.3.A The presence of toxic substances in the rye kernel

Research to date has revealed three groups of substances present in the rye kernel which could potentially be responsible for the adverse effects of a rye diet:

- i) Pentosans
- ii) Trypsin inhibitors
- iii) Alkyl resorcinols

i) Pentosans, or cereal gums, are polymers of araban and xylan sugar units, they have been shown to occur in all of the five major cereals although the pentosan concentration is higher in rye than in any of the other grains (Preece and MacKenzie 1952). Moran and McGinnis (1965) postulated that the high level of pentosans in rye might be indirectly responsible for the digestive disturbances associated with feeding the cereal to poultry (first noted by Halpin *et al.* 1936) by stimulating deleterious intestinal micro-flora. This hypothesis was based on the fact that when high levels of antibiotic were included in a rye-containing diet the adverse effects were overcome. Similar results were obtained by MacAuliffe and McGinnis (1971) and by Fernandez *et al.* (1974), however, the latter authors also reported improved protein efficiency ratios and higher weights of chicks when procaine penicillin was added to diets of corn, wheat and barley as well as rye. Moran and McGinnis (1965) proposed that the antibiotic treatment

prevented the build up of an unfavourable intestinal micro-flora in poultry. This hypothesis seems acceptable with the knowledge that digestive disturbances seem to be limited to non-ruminant species, resulting characteristically in wet sticky faeces. Hungate (1966) pointed out that ruminant species maintain a large microbial flora in the rumen which is able to break down the pentosans before they reach the intestine. Consequently they cannot stimulate an adverse micro-flora and cause similar digestive disturbances. However, before this hypothesis can be accepted, further work seems to be required to confirm the results of tests with antibiotics on non-ruminant species other than poultry, and to attempt to identify the deleterious micro-flora and their antibiotic susceptibility (Haeberle 1974).

ii) Trypsin inhibitors, named because of their ability to bind the pancreatic enzyme trypsin into an inactive complex, are proteinaceous substances first isolated from the endosperm of rye by Polanowski (1967). Minja (1970) studied six varieties or lines of Western Canadian rye and found that the level of trypsin inhibition ranged from 22.5 - 52.5% of normal enzyme activity. Chernick *et al.* (1948) attributed pancreatic hypertrophy and decreased growth rates of poultry and rats to the high levels of trypsin inhibitor present in their diet of soybean meal, but Minja (1970) could find neither decrease in growth nor pancreatic hypertrophy in chickens fed diets containing high (50%) levels of rye. Trypsin inhibitors, due to their proteinaceous nature, are heat-labile but neither Minja (1970) nor Moran *et al.* (1969) could find any improvement in the biological value of rye after heat treatment or autoclaving. To date there seems to be very little evidence that trypsin inhibitors are the primary cause of the feeding problems associated

with rye (Minja 1970).

iii) Alkyl-resorcinols, are compounds consisting of a phenolic moiety with a long carbon chain attached in the 5 position, they are relatively widespread throughout the plant kingdom (Levin 1971). An alkyl-resorcinol was isolated from the pericarp of rye by Wieringa (1967) and it was postulated that this compound was associated with the growth inhibition caused by rye diets. Alkyl-resorcinols had been identified earlier in wheat bran by Wenkert *et al.* (1964), but the levels found in rye were twice as high as those in wheat, up to 0.5%. Munck (1972) found that the average alkyl-resorcinol level of a number of rye varieties was 2-3 times higher than the mean level of wheat varieties.

Wieringa (1970) found that supplementation of diets with the alkyl-resorcinol containing fraction of rye oil resulted in decreased consumption and lower growth rates of rats. Although rye oil has a bitter taste, low palatability was not responsible for decreased consumption. Experiments were performed which involved administering the rations by stomach tube thus overcoming any palatability effects. The diet still produced decreased consumption suggesting that adverse metabolic disturbances were in some way influencing feed uptake (Wieringa 1967). Munck (1972) found an inverse relationship between body-fat gains and units of alkyl-resorcinol consumed in diets given to mice and implicated alkyl-resorcinols as inhibitors of fat absorption. Zillman *et al.* (1974) extracted the alkyl-resorcinols from triticale but could demonstrate no adverse effects of a high alkyl-resorcinol diet on weight gains of mice. Similarly, Friend (1970) could find no inhibitory effect of rye bran when added to the basal diets of rats. It is possible that



in these last reports the adverse effects of rye may have been diminished by the high levels of oil used in the diet (see Haeberle 1974). Although Haeberle deliberately used low levels of oil to avoid this possibility he could find no relationship between the level of alkyl-resorcinol in diets fed to mice and either consumption or their growth rates.

Munck (1972) points out that in 1964 Virtanen reported on some research of organic sulphur compounds in plants in which he reviews certain inhibitors to the disease snow mould (*Fusarium nivale*) which belong to a class of compounds known as benzoxazolines and are found at high levels in rye, and also in wheat endosperm. Their physiological effects on animals are not known, but along with the other substances present in the rye kernel, they remain potentially responsible for the low feeding value of rye. More chemical studies are necessary and further feeding trials need to be carried out before the factor(s) responsible for the feeding problems associated with rye can be fully elucidated.

### 2.3.B The nutritive quality of rye

Many experiments have demonstrated the high biological value of rye proteins, Munck (1972) found that rye had a high protein efficiency ratio (P.E.R.) than wheat, similar results were reported for rye bread compared to wheat bread by Strømnaes and Kennedy (1957) with rats and by Kofrányi and Müller-Wecker (1960) for humans. Kihlberg and Ericson (1964) found that rye flour promoted greater weight gains in rats than wheat flour and reviewed a number of articles that report on the superiority of rye protein over wheat protein. It is also well documented that the amino-acid balance of the rye kernel is superior to wheat having

TABLE 2. DIFFERENCES BETWEEN RYE AND WHEAT (RYE - WHEAT) IN THE LEVELS OF NINE AMINO-ACIDS AS REPORTED FROM THREE DIFFERENT SOURCES.

AMINO - ACID	REFERENCE AND UNIT OF MEASUREMENT		
	BARTNIK(1965) gm Aa/16 gm N.	MUNCK(1972) gm Aa/16 gm N.	EWART(1967) gm Aa/100 gm Total Aa.
ARGININE	+2.0	+0.36	+1.0
HISTIDINE	-0.5	+0.02	-0.1
ISOLEUCINE	-0.5	-0.05	0
LEUCINE	-0.8	-0.43	0
LYSINE	+1.0	+0.87	+1.3
METHIONINE	-0.4	0	+0.4
PHENYLALANINE	0	+0.21	-0.2
THREONINE	+0.5	+0.48	+0.7
VALINE	+0.5	+0.25	+0.7

Note; Bartnik and Munck used whole grains, Ewart used flour.

higher levels of Lysine, Arginine and Threonine but lower levels of Methionine, the ratio of essential to non-essential amino-acids being higher than in wheat (Kihlberg and Ericson 1966). Differences between wheat and rye in the levels of nine amino-acids reported from three different sources are shown in Table 2. Bartnik (1965) demonstrated that although the biological value of rye proteins is superior to that of wheat, rye proteins were 10% less digestible than wheat. Similarly Eggum (1968) using rats, obtained nitrogen digestibility figures of 77% for rye, 82% for barley, 88% for corn and 90% for wheat. Janicki and Kowalczyk (1967) concluded that an important factor affecting the feeding value of rye was the low availability of protein, and also of carbohydrates and fats, when compared to wheat and corn. Further work needs to be carried out to understand this problem and how it relates to the presence of toxic substances in rye discussed previously.

Candlish (1975) used an analogue computer to evaluate the inclusion of rye in a laying-hen diet and in a fattening-swine diet. She concluded that in both diets rye priced at 90% of the price of barley could compete with barley in formulations in amounts up to 35% of the diet. This procedure takes into account not only price but protein quality, energy value and mineral content. The computer only included higher levels of rye in a laying-hen diet when the price of rye was programmed to be exceptionally low. Candlish points out that the metabolizable-energy value of rye used when programming the computer was very low and that any increase in this property would raise its value as a feed grain since energy is the first limiting factor in most diet formulations. Research into the available literature on the metabolizable-energy of rye compared to other grains (see Table 3) has revealed that the value

TABLE 3. METABOLIZABLE ENERGY VALUES (AS FED KCAL/KG) OF RYE, WHEAT, BARLEY, OATS AND CORN WHEN FED TO FOUR DIFFERENT SPECIES.<sup>1</sup>

GRAIN		SPECIES			
		CATTLE	POULTRY	SHEEP	SWINE
RYE	MEAN	2615	2559	2695	3150
	RANGE	(2530-2735)	(2241-2888)	(2650-2735)	(3079-3208)
WHEAT	MEAN	2780	3090	2835	3322
	RANGE	(2720-2830)	(3012-3168)	(2820-2850)	(3298-3378)
BARLEY	MEAN	2556	2620*	2676	2924
		(2330-2630)		(2580-2730)	(2909-2949)
OATS	MEAN	2522	2513	2505	2670
	RANGE	(2400-2690)	(2498-2529)	(2450-2580)	(2549-2759)
CORN	MEAN	2835	3366*	3055	3067
	RANGE	(2790-2860)		(3010-3080)	(2830-3313)

<sup>1</sup> FIGURES FROM NUTRITIONAL DATA ON U.S. AND CANADIAN FEEDS (NATIONAL ACADEMY OF SCIENCE, 1971).

\*FIGURES USED BY CANDLISH(1975) BUT NOT GIVEN IN ABOVE.

used by Candlish of 2712 Kcal/kg for rye fed to swine was much lower than that documented. In fact the documented values seem to compare very favourably with the other cereals especially with respect to swine, and the results of Candlish may be slightly misleading.

## 2.4 The Future of Rye

Carmichael and Norman (1970) reviewed the Canadian rye situation and at that time could not foresee any major increase in the demand for rye on either the export or domestic market. Production seemed unlikely to increase because of the low demand resulting in depressed prices relative to other cereals, and the relatively low yields of rye. At the time barley prices were also depressed below rye, which together with the farmers traditional prejudice against rye as a feed grain did not favour its development as a cheap animal feed (Carmichael and Norman 1970). Rye prices are now much higher and with good husbandry yields of rye have been obtained which destroy the myth of rye as a low-yielding cereal (Reeves 1971). The Canada Grains Council recently recognized rye as the preferred grain crop for extensive areas of Western Canada, and especially for rotation purposes with other cereals (Canada Grains Council 1974). Its ability to outyield other cereals on light, sandy soils where nutrients and/or moisture may be limiting is now well established (Carmichael and Norman 1970, Reeves 1971).

Of the two types of rye, fall rye has a number of advantages over spring rye. It is the hardiest of the winter cereals, and its vigorous spring growth makes it valuable as a means of weed control (Principles and Practices of Commercial Farming 1974), and furthermore, it matures in advance of most annual weeds preventing shattering of weed seeds that normally carry over into the next year's crop (Reeves 1971). Including fall rye in a cropping programme allows more efficient utilization of labour and machinery, requiring high input for seeding in late fall, and for harvesting before spring cereals are ripe (Reeves 1971). It also reduces the risks associated with prolonged wet, spring-seeding

conditions and acts as a cover crop against soil erosion (Principles and Practices of Commercial Farming 1974). Spring rye is also advantageous in ripening well before other cereals.

With no foreseeable major increase in the domestic demand for rye, either as a bread grain or for use in distilling (Carmichael and Norman 1970), the future prospects of rye will depend on its increased use as an animal feed, both in Canada and on the export market. Recently the Canada Grains Council recognized the potential of rye but emphasized the need to identify and eliminate the toxic constituents of the rye kernel, and to remove the prejudice surrounding the feeding of rye before this potential could be realized (Canada Grains Council 1974).

## 2.5 Heterosis in Rye

It was towards the end of the 19th century that the phenomenon of heterosis or hybrid vigour was first shown to occur after cross-pollination of pure lines of corn. This discovery is attributed to Beal through his experiments on controlled parentage although it seems his work may have been influenced by previous work of Darwin on cross- and self-pollination in corn (Shull 1952). Prior to 1900 it was recognized that continued enforced self-pollination of corn resulted in a reduction in vigour, but it was not until after the work of Shull during 1907 that a heterosis concept was formulated combining results of inbreeding and cross-pollination (Shull 1952).

The results of Beal's work with corn were familiar to Fruwirth, who in 1913 reported that when two pure lines (varieties) of rye were artificially crossed the yield of the  $F_1$  exceeded that of the parents (Fruwirth 1913). This seems to be the first documented report of hybrid vigour in rye. One year later, Rümker and Leidner (1914) published a paper entitled "A note on inbreeding in rye." The yield components of 96 pure lines were compared to 48 cross-fertilized lines and in general the cross-pollinated lines had better germination, a higher yield per plant and higher 100 kernel weight. Similar results were obtained by Steglich and Piper (1922) and the results of these early workers were summarized by Bredeman and Heuser (1931) in a paper entitled "Notes on heterosis in rye." Their own work supported previous results, in a majority of intervarietal combinations the  $F_1$  outyielded either parent. Thousand kernel weight and ear size were the main components responsible for heterosis, although different yield components contributed to the heterotic effect in different varietal



combinations. Heterosis could also be seen in the growth of young plants in the field, measurements of fresh-weight and leaf-length revealed increases of up to 50% and 30% respectively above the best parent. They noted that the advantages of the  $F_1$  were only rarely evident in the  $F_2$  and that by  $F_4$  yields were no better than the original parents. Bredeman and Heuser (1931) also discovered that seed harvested from sowing a mixture of equal parts of two varieties showed heterosis due to the natural outcrossing between varieties, and produced a crop having a higher yield than either parent. Since these early results, many of the reports of heterosis in rye have been obtained by cross-pollination between previously out-crossed lines or varieties. In others some degree of isolation has been practiced but not complete inbreeding, and in others lines that have been fully inbred for a number of years have been used. Interest in both intervarietal and inbred-line hybrids has continued up to the present day.

#### 2.5.A Heterosis between varieties

Measurements of heterosis between varieties have been made using either seed obtained from natural cross-pollination or seed obtained by artificial emasculation and pollination techniques. For the purposes of convenience this criterion has been used to classify some of the literature on intervarietal heterosis in rye.

#### Measurements of heterosis utilizing natural cross-pollination

Schribaux (1931) sowed equal parts of the variety Petkus and a local variety, in the next year the progeny of this sowing yielded 15% more than the best parent. Similarly Heuser (1935) sowed two varieties

in such a way as to allow maximum cross-pollination between them. When conditions for cross-pollination were especially favourable a rise in the yield of the  $F_1$  could be demonstrated, when conditions were not favourable there was a decline in the yield of the  $F_1$  due to intra-varietal pollination. On the basis of these results Heuser assumed that the heterosis effect could not be utilized under practical cultivation.

Frimmel (1939) allowed some plants of long and short-grained varieties of rye to open-pollinate and ears of other plants were enclosed for self-pollination. The grains from the progeny of crosses between different types were larger and heavier than those from the progeny of self-pollinated plants. As well as a heterotic effect, a cytoplasmic effect for grain size could be detected, the grains obtained from progeny when the larger-grained parent was used as female were larger than grains from the progeny of the reciprocal combination.

Krasniuk (1946) compared the yield of plots of rye sown with stock seed to plots sown with seed obtained from plants of the same varieties previously allowed to open-pollinate with other varieties. In every case the plots sown with open-pollinated seed gave higher yields, the increase ranging from 1-96%. He suggested that new varieties could be produced by allowing varieties to open-pollinate, selecting the best progenies in the next generation and using these as the basis of a new variety. He cites the example of a new variety Volžanka, produced by this method, which outyielded standard rye varieties by up to 10%.

Kozyrj (1950) planted rye varieties so as to allow a high level of cross-pollination with other varieties. The progeny were found to be more uniform and more vigorous than the pure varieties and were also hardier, had more tillers, more productive ears and yielded up to 1.9

Q/Ha more than these varieties. Similarly Medvedev (1950) found that hybrids produced more viable seed, with a higher 1,000 kernel weight and were hardier, more productive and more vigorous than the initial varieties. Yields were found to increase again after further open-pollination and mass selection within the hybrid material was practiced to produce varieties which outyielded a standard variety by up to 3.5 Q/Ha.

Vettel and Plarre (1955) investigated the possibilities of exploiting heterosis on a commercial scale. They found that the degree of genetic diversity between parents was important to the levels of heterosis expressed and concluded that the use of hybrid rye was commercially feasible providing: a) that parents had been tested and selected on combining ability, b) there was a high level of natural cross-pollination between lines, and c) that a high yield could be obtained in the  $F_2$  as well as in the  $F_1$ .

Šestakov and Orlov (1957) produced hybrids by growing alternate rows of two varieties. The hybrid progeny had a mean yield over 4 years of 1.3 Q/Ha above the original varieties, greater hardiness and larger grain. Salimen (1959) found that open-pollinated seed of varieties had yields 10-19% above the pure varieties and exhibited similar levels of heterosis for straw yield, but no difference in winter hardiness.

Slabonski (1964) produced hybrids by open-pollination between German and Hungarian tetraploid rye varieties, he concluded that heterosis was a regular phenomenon in tetraploid rye. Increases in yield were mainly associated with better fertility and a greater number of productive ears per unit area, 1,000 grain weight remained more or less unchanged.

Pivnenko (1963) found that an intervarietal hybrid yielded 2.1 Q/Ha

higher than the best parent. Hybrids between different lines of the same variety were higher yielding than intervarietal hybrids. This was because cross-pollination between the lines was 15-50% higher than that between varieties resulting in more hybrid plants in the progeny. Bauer (1968) maximized cross-pollination by sowing the desired parents as either adjacent plants or in adjacent rows. Usually marked heterosis was only expressed in the first year, however some combinations showed heterosis over two years, and one combination showed heterosis over four years of 126, 121, 112 and 113% of the standard variety.

Measurements of heterosis utilizing artificial pollination techniques

Glušcenko (1941) allowed emasculated plants of one variety to out-pollinate with plants of surrounding varieties and found that the seed from these ears had better winter survival, larger ears, and heavier grains than the original variety. Kuznecov (1950) made intervarietal crosses and found that hybrids were superior to the plants from pure varietal seed. They showed more extensive tillering, were more productive, and were also earlier and more resistant to drought and cold. The seed of the hybrids was also found to be of better quality and it was suggested that mixing the seed of two adapted varieties would be a satisfactory method of producing hybrid seed.

Hagberg (1952) made all possible cross-combinations between three varieties and found that a high degree of tillering was responsible for the heterotic yields above that of the best parent. Height or ear-length did not exhibit hybrid vigour in these particular combinations, levels of heterosis were thought to be low as the three parents were

distantly related. Müntzing (1954) carried out a similar experiment with three tetraploid varieties and found that most yield-components were responsible for producing heterotic yields above the better parent. This was especially true for the number of florets per head, fertility, and the number of mature plants per plot. Again it was noted that levels of heterosis might be low as the parents were distantly related. Similarly, Borojevic (1959) crossed the two tetraploid varieties Petkus and Stalrag but found no significant heterosis for yield although the  $F_1$  was taller, had a higher number of kernels per head and higher 1,000 kernel weight. It was suggested that this could also be accounted for by the lack of genetic diversity between the two varieties.

Redei *et al.* (1954) made 274 crosses involving 23 varieties. At one location yield of 60 hybrids averaged 3% more than the mean yield of the 18 parents and at a second location the mean yield of 73 hybrids averaged 7.5% more than that of the 12 parents involved. Baeva (1964) found that hybrids produced by intervarietal crossing yielded up to 35% above a standard variety, improved vigour, more productive tillers, greater fertility and larger grain were responsible for the increment. Similarly, Kosov (1969) produced 18 hybrids between different cultivars and the best surpassed its better parent by 40% although only four of the eighteen excelled their better parent. Yield increases in the hybrids were due to greater 1,000 kernel weight and also to improved winter hardiness. In another study (Kosov 1970) involving 36 intervarietal hybrids, fifteen had higher grain yields than their best parent, one hybrid exceeding the better parent by 87% and 34% at two locations. Kobyljanskii and Kosov (1971) investigated 83 intervarietal hybrids and concluded that the highest yields were produced by crosses

between two high-yielding parents, although only one out of ten such hybrids displayed heterosis above the best parent.

Pfahler (1966a and b) investigated the expression of heterosis in intervarietal hybrids on a single plant basis and at various seeding rates under solid-seeded conditions. He used three varieties of rye and crossed them reciprocally to obtain six  $F_1$  populations. On a single-plant basis he found that heterosis above the best parent was expressed for both plant weight and grain yield, there being considerable differences in the combining ability of the parental varieties. The level of heterotic response was also influenced by the direction of the cross and the year in which the test was carried out. Under solid-seeded conditions only one of the hybrids showed heterosis above that of the best parent and Pfahler assumed that the level of heterosis under space-planted conditions was not completely related to solid-seeded performance. In the same experiment composite populations were formed by mixing equal quantities of hybrid seed and seed of one of the varieties. Similar composites would be formed naturally when two varieties are mixed and sown together, containing 50%  $F_1$  individuals and 25% of either parent (assuming that self-incompatibility prevents self-fertilization). In some cases the performance of this composite population compared favourably to that of the  $F_1$  population. Pfahler (1966b) suggested that as no form of male sterility had been isolated in rye, production of populations containing 100%  $F_1$  individuals would be difficult. The production of such composite populations would be possible on a large scale by mixing varieties and could be used as a means of utilizing heterosis in rye. This was earlier suggested by Bredeman and Heuser (1931).

### 2.5.B Heterosis between inbreds

Peterson (1934) although not the first to study inbreeding effects in rye, seems to have been the first to suggest that pure lines of rye could be established, after selection for desirable characteristics, and utilized to take advantage of the heterotic effect between them. These lines could be maintained in small isolated plots and a hybrid population produced by growing two of these lines together and allowing them to outcross. This had been previously suggested and practised by Schribaux (1931) with varieties, not with inbred lines. Peterson suggested that just a few pure lines selected from a single variety would prove to be satisfactory source material.

Nilsson (1937) investigated inbreeding in rye and noted an increase in the yield of the  $F_1$  following pollination between lines, in  $F_2$  yield was only 76% of the original variety. He was attempting to find a method which would allow maximum genetic differentiation between two lines without depression in vigour. He did not follow the technique any further because of the depression in vigour caused by enforced selfing. Leith and Shands (1938) were also investigating inbreeding and found that inbred lines, when allowed to outcross, produced hybrids which were much more vigorous than plants of an open-pollinated variety. Prjaniškova (1939) crossed plants inbred for six generations. The  $F_1$  plants were very vigorous and further inbreeding of the lines resulted in even more luxuriant  $F_1$ 's but reduced fertility in the  $F_2$  was taken as evidence that no useful results could be obtained through inbreeding and the crossing of inbred lines.

Krasniuk (1941) reviewed 12 years of inbreeding work with rye and concluded that the method was of no practical value as inbred lines were

unable to compete with out-pollinated material. They were very short, tillered poorly, had poor quality grain, and showed poor germination and winter-hardiness. Crosses were made between a large number of lines but no favourable combinations were discovered. However, seed from the free crossing of varieties was reported to give higher yields and a higher grain-weight than the original varieties.

Müntzing (1943) used lines inbred for seventeen generations to investigate the possibility of using the double-cross method in rye on account of the successful results obtained by maize workers using this technique. Height, plant weight and kernel weight per plant were all higher than a control population, the latter two characters by 20% and 14%, respectively. Germination percentage and fertility of the double-cross hybrids were lower. The double-cross hybrids were at least as good as the  $F_1$  hybrids and Müntzing thought it possible that even better results could be obtained if systematical cross-combinations were made involving a larger number of lines. He proposed that a number of the best (primary)  $F_1$  combinations could be maintained as separate populations to avoid the problem of inbreeding depression. Seeds from these populations could be mixed to allow spontaneous hybridization in the next generation producing hybrid seed. He concluded that his results warranted testing the method on a larger scale.

Mayer (1944) reported on extensive experiments which utilized inbreeding in an attempt to improve Petkus rye. He was able to obtain relatively vigorous lines of high self-fertility which reached an inbreeding minimum after an unspecified number of generations, this was assumed to indicate homozygosity. Crosses between inbred lines exhibited heterosis, which was relatively highest in the most weakened



lines. On further multiplication yields fell to below the level of the original Petkus as a result of self-pollination in the self-fertile material. Although the weakest inbreds showed the highest relative levels of heterosis, the better hybrids were obtained from crosses of two good inbred lines.

With a thought to using natural outcrossing between inbreds to produce hybrid seed, Ferwerda (1951) investigated the degree of self-pollination of a number of inbred lines. He did this by allowing natural cross-pollination to occur when an inbred plant was surrounded by an open-pollinated variety. The progeny of this plant were then grown out and could be easily classified as being derived from either selfing or outcrossing by their vigour. Some lines consistently showed a high level of outcrossing, whereas in others self-fertilization predominated. A third group were characterized by variable behaviour in different years. Further experiments demonstrated that the high level of self-fertilization in some lines was not due to the loss of the self-sterility mechanism, instead it was suggested that some degree of cleistogamy had been unconsciously bred into these lines. The importance of this factor in relation to producing a hybrid variety was noted, only male-sterile types offer a chance of ensuring complete cross-pollination. Geiger and Schnell (1970b) also investigated the proportion of selfing in previously inbred lines which were allowed to out-pollinate. Among 41 inbred lines the proportion of selfing varied from 4.3% to 85.9% over four years, agreeing with the results of Ferwerda (1951).

Lundquist (1966) carried out a thorough investigation of heterosis between inbred lines. He used six lines of the variety Steel that had been inbred for at least twenty-five generations. He produced their

six autotetraploid derivatives and made all possible  $F_1$ 's and  $F_2$ 's at either ploidy level and all possible double-crosses between  $F_1$ 's. This material was analyzed for nine characters (height, straw diameter, number of spikes, straw weight, number of spikelets, seed-setting, mean kernel weight, kernel yield per head and total kernel yield) heterosis was found for all the characters at both ploidy levels. The advantage of the double-cross over the single-cross was insignificant at the diploid level but quite significant at the tetraploid level. Diploid hybrids were more sensitive to inbreeding than tetraploid as evidenced by measurements taken on the  $F_2$ 's. Although high levels of heterosis were found, only two of the hybrids at the diploid level had yields superior to the original cross-pollinated strain, none of the double-cross tetraploid hybrids had yields approaching that of the cross-pollinated tetraploid strain.

Wolski (1968) reviewed some of the problems concerning utilization of hybrid rye. He concluded that genes connected with yield were in a state of balanced heterozygosity and that the possibilities of improvement through the application of heterosis were limited. Wricke (1973) however, investigated inbreeding depression and gene-action in rye. He found no indication of epistatic gene action, and a high degree of dominance for grain yield. He proposed that this fact suggested the advisability of breeding hybrid rye varieties.

A conference on the study and use of heterosis in rye was held in Leningrad in 1973 (Gaspar 1973). Work on heterosis in rye seems to be underway in many European countries and intervarietal hybrids were reported which outyielded their best parents by 46-57%, and a standard variety by 67-110%. Much of this work has been with intervarietal

crosses rather than with inbred lines. Material with good combining ability has been used to produce synthetic varieties, however, no true hybrid variety has been released.

## 2.6 The Genetic and Physiological Basis of Heterosis

Since just after the turn of the century, after the concept of heterosis and inbreeding depression had been formulated, two theories were proposed for the genetic basis of heterosis. Davenport (1909) attributed inbreeding depression to the exposure of deleterious recessive alleles and heterosis to the masking of these alleles by dominant alleles produced by crossing two unlike inbred lines. Shull (1908) and East (1908) attributed heterosis to the heterozygous condition *per se* of the genes of a hybrid relative to the homozygous condition of the genes of an inbred. These two hypotheses became known as the dominance and overdominance hypothesis, respectively. The merits of these hypotheses have been fully discussed elsewhere (Crow 1952, Allard 1966, Briggs and Knowles 1967). Briggs and Knowles also include the theory of epistasis (inter-allelic gene action) as a possible explanation of heterosis. Despite the time that has elapsed since these proposals were made there is no evidence that singles out any one of them as the basis of heterosis. However, current opinion is of the view that these theories are not naturally exclusive, and that there is no reason why the complex phenomenon of heterosis should result from a single genetic cause (Briggs and Knowles 1967).

Attempts have been made to relate these theories of heterosis to a physiological basis. In support of the dominance theory many deleterious genes are known to be exposed on inbreeding which are hidden by the heterozygous condition, e.g., chlorophyll mutants. The theory assumes that other subtler mutants exist which affect vigour and yield and are exposed on inbreeding and hidden by hybridization. In support of the overdominance theory, a number of cases are now documented of

heterozygosity at a single gene being advantageous relative to the homozygous condition (Strickberger 1972). Attempts have been made to explain this in terms of the advantages of two gene products, a hybrid gene product, or a more optimum amount of a gene product produced by the heterozygous locus (Strickberger 1972). Similarly epistatic effects such as complementary, inhibitory and duplicate gene interactions are known (Briggs and Knowles 1967) and could contribute to the heterotic effect as interallelic interactions.

In a recent paper Kirk and Jones (1974) utilized inbred lines and  $F_2$ 's of rye in an attempt to investigate chemical and physiological changes in the nucleus that occur when genes are in the heterozygous condition. They used four lines that had been inbred for over 40 years and made a number of crosses between these lines. Measurements were made on certain nuclear characters, nuclear protein, nuclear RNA and histone. Hybrids were found to have greater amounts of nuclear protein, in some cases almost 50% more than inbreds during the early stages of growth. Similarly hybrids were found to have about 25% more nuclear RNA than inbreds. Again this was in the first few days of growth, the differences decreased as the plants aged. These changes in the nuclear phenotype are obviously closely paralleled by the differences in the growth pattern of inbred and hybrid rye viz. inbreeding depression and hybrid vigour. Levels of nuclear histone were found to be inversely proportional to both nuclear protein and RNA, being lower in hybrids than in inbreds. This result seems to confirm the theory first proposed by Huang and Bonner (1962) that histone acts as a suppressor of chromosomal RNA, and hence protein, synthesis. Polyakova *et al.* (1971) have similarly found greater amounts of histone in the pollen nuclei of

inbred lines of radish relative to cross-pollinated lines. This relationship in both rye and radish could be a consequence of inbreeding, or alternatively inbreeding depression could be a consequence of increased levels of histone. The basic mechanism which relates the condition of genes to the level of histone still remains elusive (Kirk and Jones 1974), however further research in this area may lead to a better understanding of the phenomenon of heterosis.

## 2.7 Estimating Levels of Heterosis

In rye, as with many other crops, hybrid seed has to be obtained by hand-emasculatation and pollination as incorporation of male-sterility, if available, is not feasible merely to test the yield of a particular hybrid, and as yet no suitable chemical sterilants are available that can guarantee 100% sterility. With this limitation, the number of hybrid seed that can be produced for yield testing is usually minimal. As a consequence, hybrid performance has often been tested using spaced plants, small plots, or hills. As in early generation testing it is questionable how well these methods relate to performance in the field.

Hagberg (1952) when yield testing intervarietal rye hybrids spaced 10 plants 15 cms apart with 10 cms between rows and was able to replicate four times. Müntzing (1954) also with intervarietal hybrids, obtained enough seed for 30 plants per row, 5 cms between plants with two rows of each hybrid replicated three times. Müntzing (1943) seems to have been the first worker to attempt to yield test hybrids from inbred lines. The number of seed in a line varied from 187 to 17 and these were sown as "closed rows", no replication was used and yield was expressed on a per plant basis. Lundquist (1966) also worked with hybrids from inbred lines. Enough seed was obtained for two replications with 10 plants per row, 10 cms between plants and 15 cms between rows.

Pfahler (1966b) noted that most previous studies on heterosis in rye had only utilized spaced plants and proposed that the level of competition, as well as not relating to field conditions, might also alter the direction and magnitude of heterosis expressed by a line. He performed an experiment with intervarietal hybrids planted at various densities (10, 30 and 50 seeds per row foot). The results led him to

conclude that at these levels of population density all populations responded to heterosis equally and in the same direction finding no supporting evidence for his hypothesis. However, the lowest density used by Pfahler of 10 plants per row foot (3 cms between plants) was still much higher than those used by other workers. Zeven (1972) undertook a similar experiment with wheat hybrids at densities of 32, 64, 128 and 256 plants/m<sup>2</sup> and also found no effect of density on the expression of heterosis. His review of other work with wheat also supports the hypothesis of no effect of density on heterosis with one exception, some work of Rosenquist in 1931. Zeven found his own results difficult to understand and pointed out that published percentages of heterosis of 200+ over the higher parent are unlikely under field conditions and proposed that his results would not hold for densities more extreme than those he had used.



## 2.8 Cytoplasmic Male-Sterility in Rye

In 1954, Dr. E. D. Putt reported on an investigation of the cytogenetics of sterility in rye (Putt 1954). With respect to one particular inbred line he wrote "... this sterility was inherited through the female side in all crosses with other inbred lines." After allowing this line to out-pollinate he proposed that, "The genes causing sterility could have been recessive to the genes (which restored fertility) carried by the particular gamete which entered the zygote." This seems to be the first documented report of a cytoplasmic male-sterility/restorer gene system. Unfortunately it seems this work was not carried any further, however Kobylanskii (1968) again reported on cytoplasmic male-sterile forms of rye.

In the years 1966 and 1967 Kobylanskii isolated 140 male-sterile forms, mostly in ancient Russian cultivars or weedy forms of rye. When these sterile plants were pollinated with various fertile plants the progeny ranged from 70% fertile plants in some lines to all sterile plants in others. Restorers were much more frequent than maintainers. When steriles were crossed with restored steriles equal numbers of fertile and sterile plants were obtained, when two restored steriles were crossed three fertiles were obtained for every sterile. These results suggested that a single dominant gene was responsible for restoring fertility. Kobylanskii and Katerova (1973) report on another form of male sterility that requires more than one gene to restore fertility.

Another form of cytoplasmic male-sterility was discovered by Geiger and Schnell (1970a), they found male-sterile segregates in four  $S_1$  lines derived from crosses between plants of "Pampa" rye pollinated with an

inbred line. These sterile plants were sib-mated or allowed to open-pollinate and the progeny were crossed with inbred lines. Plants from these crosses exhibited various degrees of sterility from 0-100%. By backcrossing to the inbred lines completely sterile forms were obtained, backcrossing to restored sterile plants resulted in varying proportions of fertile, male-sterile and partially male-sterile plants. Geiger (1972) investigated the ability of thirteen inbred lines to restore fertility, two lines proved to be fully effective in restoration, eight lines were classified as being non-restorers, the genetics of fertility restoration for this system have not been reported. Geiger (1971) reported on another form of C.M.S. discovered when plants of a primitive Persian rye were pollinated with an inbred line of Petkus. Both sterile and fertile progeny resulted from this cross and the sterility could be maintained by crossing to non-restorer types.

Another form of C.M.S. was reported by Lapinski (1972). He made reciprocal crosses between a rye cultivar and a strain of *Secale montanum* Guss. After two backcrosses, with the cultivar as female, six out of seven plants were male-sterile but set seed when crossed. This material had the germplasm of *S. montanum* in the cytoplasm of *S. cereale*.

Lapinski further reports that the fertility was restored by one dominant gene and that an identical system also existed with *S. kuprijanovii* germplasm in *S. cereale* cytoplasm.

As Geiger and Schnell (1970a) realized, the discovery of cytoplasmic male-sterility systems in rye has provided the initial material required to test the feasibility of hybrid-rye production on a commercial scale.

### 3. MATERIALS AND METHODS

#### 3.1 The Production of Hybrids and Multiplication of Inbreds

In the winter of 1973-74 seed was available of a large number of lines of spring rye inbred for three or more generations. Twelve of these lines were selected for this study on the basis of having relatively large, plump seed. As no records of their vigour or yield had been kept it was hoped that this selection would ensure that the more vigorous lines were used, precaution was also taken to avoid selecting related lines. The twelve inbred lines, their origin and seed type are listed in Table 4.

Eighteen seeds of each line were selected and planted in the glass-house in six-inch pots, 2 seeds per pot, in late January 1974. Emergence was recorded 12 days later and missing plants or albino seedlings were replaced with some of the original seed. Tillering of the plants and their general vigour were recorded in early March and the mean number of days to heading of each line was estimated and recorded. Pollination between lines began in mid-March, no plan of the crosses to be made was attempted as there was no prior knowledge of the lines, instead crosses were made between lines that were heading at similar times. The crossing technique used was to emasculate heads of the desired female parent 2-3 days after they had emerged from the sheath, a few days before anthesis. It was found satisfactory just to clip each spikelet of the head so as to remove approximately one-third or more of each of the anthers without damaging the stigma. This avoided the tedious task of normal emasculation by removing the anthers completely. If emasculation was performed too early there was a tendency for the exposed

TABLE 4. THE ORIGIN AND SEED TYPE OF THE TWELVE INBRED LINES  
CHOSEN AS PARENTS.

LINE NUMBER	U.OF M. ACCESSION NUMBER AND ORIGIN	SEED TYPE (SIZE, COLOUR, APPEARANCE)
23-4	2D34-4 PETKUS, C.A.N. 1983, CANADA.	SMALL, BLUE, SHRIVELLED.
28-10	2D100-4 MINUSINSKAYA, RUSSIA.	SMALL, YELLOW, SMOOTH.
95-6	2D144 MARCO-JUAREZ, MEXICO.	MEDIUM, YELLOW, SHRIVELLED.
192-1	2D214-2 PETKA, GERMANY.	MEDIUM. SEGREGATING, SHRIVELLED.
194-1	2D117-1 O.J. RYE, CANADA.	MEDIUM, BLUE, SMOOTH.
195-3	2D2-4 P.I. 168133, TURKEY.	MEDIUM, BLUE, SMOOTH.
199-1	2D13-2 FRENCH, ISRAEL.	MEDIUM, YELLOW, SMOOTH.
219-1	2D29-2 3836, C.A.N. 1979, CANADA.	MEDIUM, YELLOW, SMOOTH.
252-2	2D82-3 PROLIFIC, (SELF-FERTILE) CAN.	MEDIUM, BLUE, SHRIVELLED.
361-2	2D148 P.I. 289587, MEXICO.	MEDIUM, BROWN, SHRIVELLED.
363-5	SFP-1 PROLIFIC, (SELF-FERTILE) CAN.	SMALL, SEGREGATING, SHRIVELLED.
372-5	SFP-3 " " "	MEDIUM, SEGREGATING, SMOOTH.

stigma to dry out, if too late then the nearly mature stigma could be easily damaged. After emasculation the ears were enclosed in wax-paper bags until ready for pollination.

Ears of the male parent were isolated with wax-paper bags as soon as they emerged from the sheath. During anthesis pollen was collected in the bags so it was necessary to close them firmly. Pollination was brought about by inverting the pollen-containing bag over the emasculated head of the female parent. To ensure that only fresh pollen was used, unused pollen was emptied from the bags each day. By this technique the ear of the male parent not only acted as a pollen donor, but could also be used as a source of selfed seed, along with the other isolated ears of that line. Using this crossing procedure thirteen different crosses were made with at least six heads per cross-combination.

### 3.2 Yield Testing the Hybrids

The size of the yield test was limited by the number of hybrid seeds available. The minimum number of seeds in any one cross-combination was 160; consequently it was decided that the plots would be arranged as four completely randomized blocks, each plot consisting of a row four feet long containing forty seeds, the rows being one foot apart. Within each block inbred lines and hybrids were randomly arranged, one control plot of each of Prolific and Gazelle (rye varieties), U.C.85 41 (an advanced triticale line), and Neepawa (a wheat variety) were also included in each block. It was decided that every other plot be sown to the wheat variety Norquay so that each experimental plot had a row of Norquay on either side of it. This would equalize the competition effects on the experimental plots, and it was also thought that being a semi-dwarf variety the Norquay would allow adjacent rye plots to be easily distinguished and separated should lodging occur.

The complete experiment was sown on May 15th. Included in the yield trial were thirteen hybrids and eleven of the twelve original inbred lines, one inbred line produced such a small amount of seed that it could not be tested. Prior to sowing, the 40 seeds of each inbred, hybrid and control were weighed, primarily to see whether there were any differences between the two types of seed, hybrid and inbred.

The following characters were evaluated during the experiment:-

- 1) emergence
- 2) days to heading
- 3) number of productive tillers
- 4) height

- 5) self-fertility
- 6) head size
- 7) open-pollinated fertility
- 8) one hundred kernel weight
- 9) yield
- 10) yield relative to adjacent plots of Norquay.

After heading, six ears of the hybrids, the inbreds and the rye varieties were enclosed in wax-paper bags in order to estimate self-fertility, and also to preserve the identity of some seed from both hybrids and inbreds. Before harvest, 10 open-pollinated heads of main tillers were collected to estimate the number of florets per head and the level of fertility under open-pollinated conditions of all lines. The plots were then harvested by hand and threshed in the field. After open-pollinated fertility had been taken from the ten heads the seed was recombined with the bulk from the plot and the yield of each plot obtained and one hundred kernel weight estimated. All plots of Norquay were also harvested and weighed and their identity was maintained so that an estimate could be made of the yield of each experimental plot relative to the two adjacent plots of Norquay. This was done in an attempt to estimate the value of such a measurement as an estimator of the rye yields by taking into account soil variability.

### 3.3 The Early Growth of Inbreds and Hybrids

After planting the field trial, there remained seed of some of the hybrid lines and of all of the inbred lines. This seed was used in a simple experiment to determine whether there were any differences between the early growth of hybrids and that of inbreds. Space was available in a growth cabinet adjusted to an eleven hour light period at 15°C and a thirteen hour dark period at 5°C. This environment was thought to be suitable for the purposes of this experiment and on June 4th the seed of five hybrids and eight inbreds was planted in six inch pots, five seeds per pot. Enough seed was available for three pots of each of these lines which were arranged in the cabinet as three replicates. After emergence the number of plants per pot was reduced to the four most uniform. Plant height was measured on June 12th. On June 20th and again on June 28th lengths of the first and second leaf were measured. On July 11th plant height (to the tip of the longest leaf) leaf width (at the widest point of the longest leaf) and the number of tillers per plant were measured. Plants were then harvested and oven-dried for 24 hours at 85°C and dry weight estimated.

Results of the field experiment were analyzed by computer using a programme designed by Dr. R. Baker. The statistical procedure for planning one degree-of-freedom comparisons was obtained from Snedecor and Cochran (1973). Correlation matrices were generated by computer using Statistical Package #17 of the Computer Centre, University of Manitoba. For the second experiment, the mean value over replicates for each character was calculated and inbreds were compared with hybrids by a one-way analysis of variance using the Hewlett-Packard programable calculator 9810A and standard analytical procedures.



## 4. RESULTS AND DISCUSSION

### 4.1 Characteristics of the Inbred Lines

The inbred lines were observed three times, each time in a different environment, the glasshouse, the field, and the controlled environment cabinet. During the growth of the twelve original lines in the glasshouse measurements were made on five characters, these are shown in Table 5, notes were also made on the vigour and appearance of the twelve lines. Only eleven of the lines could be used in the field experiment as the twelfth (361-2) proved to have very low self-fertility (Table 5) and did not produce enough seed to be replicated four times. Values of eleven characters of the inbred lines when grown in the field are given in Table 6. Remnant seed of eight of the inbred lines was included in the growth analysis experiment carried out in the controlled environment cabinet, the results of the experiment are given later in Table 10.

In the glasshouse germination of the inbred lines varied 100% to less than 50%. Two of the twelve lines produced albino plants and one line 361-2, produced two plants whose early leaves were longitudinally striped, however the latter leaves were normal. Under field conditions emergence varied from 86% to 57% with a mean for the eleven lines of 74.7%, albino plants also appeared in the field but were not recorded. In the glasshouse a count was made of the number of tillers per plant and there were quite large differences between lines, some being very vigorous, e.g. 194-1 and 195-3 with 5.45 and 5.90 tillers per plant respectively. Others, such as 23-4 and 199-1 had only 2.57 and 2.25 tillers per plant respectively (Table 5). The number of fertile tillers

TABLE 5. CHARACTERISTICS OF THE TWELVE INBRED LINES WHEN  
GROWN IN THE GLASSHOUSE.

LINE NUMBER	CHARACTER				
	GERMINATION (18 SEEDS)	TILLERS/ PLANT	DAYS TO HEADING	SELF FERTILITY%	FLORETS/ HEAD
23-4	10(+6A)*	2.57	49	37.2	63.0
28-10	18	3.05	46	46.7	49.2
95-6	10	4.12	49	41.6	53.3
192-1	15	4.00	51	48.4	54.4
194-1	14	5.45	56	65.1	60.9
195-3	7	5.90	51	59.7	52.0
199-1	9(+3A)	2.25	46	49.9	55.1
219-1	17	4.70	51	54.9	64.6
252-2	14	3.00	51	48.1	52.0
361-2	10	3.89	48	2.2	39.4
363-5	17	3.22	46	53.4	41.7
372-5	16	3.23	45	68.8	43.1

\*A=ALBINO PLANTS.

TABLE 6. VALUES OF ELEVEN CHARACTERS (MEAN OVER FOUR REPLICATES) OF THE ELEVEN INBRED LINES WHEN GROWN IN THE FIELD AS PART OF THE FIRST EXPERIMENT.

LINE NUMBER OR NAME.	CHARACTER										
	WEIGHT OF ORIGINAL SEED (gms): <sup>1</sup>	EMERGENCE (%)	DAYS TO HEADING.	FERTILE TILLERS /PLANT.	HEIGHT (cms).	FLORETS /HEAD.	OPEN-POLLINATED FERTILITY(%)	SELF-POLLINATED FERTILITY(%)	YIELD GMS	YIELD % OF NORQUAY.	HUNDRED KERNEL WEIGHT.
23-4	1.08	73.25	52.3	2.31	79.0	53.85	42.84	12.93	17.63	14.57	3.73
28-10	0.93	71.25	51.3	1.95	83.0	49.40	57.23	50.15	17.50	15.82	3.72
95-6	1.08	57.00	52.0	2.82	68.3	42.90	50.68	18.56	15.13	11.57	4.17
192-1	1.10	76.25	54.0	2.55	77.3	50.17	65.45	50.84	32.25	32.97	4.92
194-1	1.18	80.75	52.3	2.85	93.8	53.00	78.60	65.77	59.77	47.85	4.72
195-3	1.26	78.75	52.3	2.03	88.3	52.12	58.42	29.22	26.00	21.70	4.39
199-1	1.17	72.00	50.5	2.29	80.0	53.15	64.25	0	27.38	24.42	4.42
219-1	1.23	77.50	51.8	2.87	77.3	53.07	58.14	40.24	27.63	19.35	3.94
252-2	0.86	62.50	50.5	2.08	76.0	45.05	58.10	42.18	14.88	12.82	3.31
363-5	0.82	86.25	48.8	1.67	49.3	38.77	46.89	35.14	9.38	8.75	2.67
372-5	1.08	86.25	49.3	1.96	75.3	39.52	63.68	55.96	20.00	17.42	3.97
MEAN	1.07	74.70	51.4	2.31	77.0	48.27	58.57	43.45	24.32	20.66	3.99

<sup>1</sup>MEAN OF FOUR SAMPLES OF FORTY SEEDS.

<sup>2</sup>MEAN OF FOUR EARS OF EACH LINE.

per plant was also recorded on the material in the field and seems to show very little relationship to measurements made in the glasshouse, presumably because plants in the glasshouse were not under competitive conditions. Again there were relatively large differences between lines, ranging from 1.67 to 2.85 fertile tillers per plant, some of the differences between inbreds were significant (see Appendix I).

Days to heading of the inbred lines was recorded in both the glasshouse and the field. There was much variation among the lines under both environments but correlation between the two sets of data was not significant ( $r = 0.4111$ ) although the four earliest lines in the glasshouse were among the five earliest in the field. The inbred lines headed over a period of 10 days in the glasshouse and over 6 days in the field. Height of the inbred lines was not measured in the glasshouse although there were considerable differences, two lines 363-5 and 372-5 were considerably shorter than the others. Height was measured in the field and there were significant differences (see Appendix I). Lines 363-5 and 372-5 were again among the shorter lines but all lines were considerably shorter in the field than in the glasshouse. This could possibly be due to the extra generation of inbreeding of the field material although it is perhaps more likely due to environmental differences.

Head size, as measured by the number of florets per head, was measured in both the glasshouse and the field material, the correlation between the two sets of data was significant ( $P = 0.01$ ,  $r = 0.6899$ ). From the field data only, there was also a significant correlation between height and head size ( $P = 0.05$ ) (see Appendix II). Open-pollinated fertility of the inbreds was measured under field conditions

and varied from 42% to 78%, this character was also correlated with height ( $r = 0.518$ , see Appendix II) but not significantly so. The interrelationships of these three characters would seem to suggest that all three are affected by inbreeding to similar degrees.

Self-fertility of the inbred lines was measured by bagging heads in both the glasshouse and the field. The mean fertility of the inbred lines was slightly higher in the glasshouse than in the field. When the two sterile lines (361-2 in the glasshouse and 199-1 in the field) are not included the correlation between glasshouse and field data is high ( $r = 0.7562$ ) and significant ( $P = 0.01$ ). Line 361-2 was virtually sterile in the glasshouse and so was not grown in the field, it seems unlikely that this was representative of the line as adequate seed had been produced in the previous generation, however it could be that unrepresentative, incompatible plants were selected for selfing. Line 199-1 was about 50% fertile in the glasshouse but was completely sterile in the field. Again this could be due to unrepresentative, incompatible plants being bagged, although as four plants were bagged this seems unlikely and a more plausible explanation is that plants were bagged which due to localized conditions in the field were male-sterile. Such conditions did prevail in certain areas due to droughting and cracking of the ground.

Yield of the inbreds under field conditions varied considerably from 9.38 to 59.77 gm, it was highly correlated with open pollinated fertility ( $P = 0.01$ ) and also with height ( $P = 0.05$ ) and one hundred kernel weight ( $P = 0.05$ ) (see Appendix II). One hundred kernel weight was also significantly correlated with the weight of the forty original seed sown in the field, and also with days to heading. The latter correlation would suggest that seed size is partially dependent on the length

of the growing season of the inbred.

The initial material used in this project was known to have been selfed at least four times before being grown in the glasshouse. Research into the origin of the material revealed that some lines had undergone considerably more inbreeding than this. Three lines, 252-2, 363-5 and 372-5 were found to have been derived from Prolific rye. The line 252-5 was first accessioned at the University of Manitoba in 1959 as a self-fertile selection of Prolific. Presumably this line must have undergone some inbreeding prior to that date to have allowed selection for self-fertility. The lines 363-5 and 372-5 were derived from 252-2 as self-fertile selections and must have undergone further selfing before the most recent four generations of inbreeding. Consequently, three of the lines are known to have been inbred more than four times, and it is possible that other lines had also undergone inbreeding prior to the last four generations. The level of inbreeding in these three lines can perhaps be estimated. Prolific rye was accessioned at the University in 1956 and line 252-2 was accessioned three years later in 1959 and so is unlikely to have been inbred more than three generations during that time. The other lines were derived from this by further selfing an unknown number of times. With the four most recent generations of selfing it seems reasonable to assume that line 252-2 has undergone 5-7 generations of inbreeding prior to the experiment and lines 363-5 and 372-5 a minimum of six or seven generations.

A number of workers have investigated inbreeding in rye, both Sybenga (1958) and Wolski (1970) have followed the results of inbreeding starting from an initial outbred population. Sybenga found that after five generations of inbreeding plant weight, plant height and

the percentage of fertile pollen decreased by 20, 35 and 40% respectively relative to the original population. The number of tillers per plant and seedset after selfing increased by 30% and 60%, respectively. Wolski (1970) carried out a more extensive investigation up to the 7th inbred generation. In his material all characters measured showed a decrease, most severely affected were weight of grain per plant, productive tillers, number of grains per head and 1,000 grain weight. To a lesser extent height, number of florets per head and head length were decreased. These results appear to be in agreement with others who have not followed inbreeding depression but have compared inbred lines to the original population, e.g. Müntzing (1943) and Lundquist (1966), and also with Wricke (1970) who followed inbreeding for 3 generations after crossing. The latter author estimated values for the inbreeding depression minimum of yield, plant height, and thousand grain weight as 24-34%, 91-96% and 67-78%, respectively.

Because no out-pollinated source material of the lines used in the present study was grown it is difficult to determine which characters have been affected by inbreeding depression and to what degree. However, the inbred lines can be compared, with caution, to the varieties Gazelle and Prolific with the understanding that these are adapted varieties unrelated genetically to the inbreds (except for the three lines derived from Prolific). Comparison of the inbreds with the thirteen hybrid lines can also be used as a measure of inbreeding depression. From Table 8, it seems that the inbred lines could be characterized as having small seed, a low tillering capacity, a low number of florets per head, a low level of fertility under open-pollination but high self-fertility, and finally a low yield. These seem to be in

agreement with other workers. Two lines 363-5 and 372-5 are thought to be more highly inbred than the others, observations tend to support this theory. These two lines and to a lesser extent line 252-2 which is also likely to be highly inbred, appeared to be much weaker than the other lines in the glasshouse, being short and having narrow leaves and weak culms which could not support the head erect. These results were supported by observations in the field, lines 363-5 and 372-5 were short, had poor tillering and small heads (see Table 6), line 363-5 was generally much weaker than 372-5. It is also interesting to note that these lines showed good germination and emergence in both the glasshouse and field and did not produce albino plants. This could be indicative of their highly inbred nature, strong selection having occurred over time against deleterious characters.

The other lines although not as highly inbred as 363-5 or 372-5 often were as weak as them in certain characters. Line 28-10 had small seed and tillered poorly, line 95-6 was short, had small heads and very poor emergence. Lines 192-1, 194-1, 195-3 and 219-1 were all relatively vigorous with large seed, good tillering, large heads and good fertility. The more vigorous higher yielding lines tended to be later, the two highly inbred lines were early, perhaps a reflection of a high level of inbreeding or perhaps due to the fact that they were both derived from Prolific which was also early. The open-pollinated fertility of the inbred lines was much lower than that of the out-pollinated controls, and was especially low for 23-4, 95-6 and 363-5, three lines which yielded poorly. Line 194-1 which had high open-pollinated fertility was the highest yielding of the inbreds, it also had the second largest one hundred kernel weight, good tillering and large heads.



Although lines 252-2, 363-5 and 372-5 were self-fertile selections (see earlier) their self-fertility was not exceptionally better than the other inbred lines. Self-fertility in the field was much more variable than in the glasshouse, three lines 23-4, 95-6 and 199-1 having greatly reduced self-fertilities while others such as 28-10, 192-1 and 194-1 were as fertile as in the glasshouse. Decreased self-fertility could be due to localized environmental effects as already mentioned.

From these results of observations on a number of characters of the inbreds it is obvious that genotype, as well as inbreeding, plays a considerable part in determining the characteristics of a line. As the level of inbreeding cannot be stated with certainty it is impossible to say whether the vigorous, high-yielding lines were so because of a tolerance to inbreeding [such lines have been reported by Brewbaker (1926) and Nilsson (1921)] or because the level of inbreeding was still insufficient to have significant effects. As the initial populations from which the lines were obtained have not been observed conclusions about the effects of inbreeding are necessarily limited.

#### 4.2 Comparison of Inbreds, Hybrids and Out Pollinated Control Varieties

From the literature there seems to have been only two previous investigations of hybrid vigour in rye which utilized inbred lines, and which also gave a full report of the characteristics of both hybrids and of an outbred population as control. Müntzing (1943) produced double-cross hybrids of inbred rye, and Lundquist (1966) carried out an extensive investigation of single-cross and double-cross hybrids at both the diploid and tetraploid level. In both cases the inbred lines were originally derived from the variety Stalrag by Professor Nilsson-Ehle and had been inbred 17 and 25 generations, respectively. In each experiment an outbreeding population of Stalrag was also grown for comparison.

Some comparisons can be made between the results of these two workers and those of the present experiment, however, certain differences must be taken into account. The inbred lines used in the present work were not as highly inbred as those used by Müntzing or Lundquist and not all were derived from one variety but from a number of different sources. Both these factors could effect the levels of heterosis. In the present experiment comparisons are made with Gazelle, an unrelated and also an adapted variety, whereas many of the inbred lines were derived from unadapted introduced material of unknown yielding ability. The results of measurements taken on the hybrids are given in Table 7 and the means of inbreds, hybrids and controls are given in Table 8.

The first character to be measured was the weight of seed obtained from self and cross-pollination in the glasshouse. It was thought important to do this in order to ascertain whether seed obtained from cross-pollination was any different in size from that obtained by self-

TABLE 7. VALUES OF ELEVEN CHARACTERS (MEAN OVER FOUR REPLICATES) OF THE THIRTEEN HYBRID LINES WHEN GROWN IN THE FIELD AS PART OF THE FIRST EXPERIMENT.

LINE NUMBER OR NAME.	CHARACTER										
	WEIGHT OF ORIGINAL SEED (gms): <sup>1</sup>	EMERGENCE (%)	DAYS TO HEADING.	FERTILE TILLERS /PLANT.	HEIGHT (cms).	FLORETS /HEAD.	OPEN-POLLINATED FERTILITY(%) <sup>2</sup>	SELF-POLLINATED FERTILITY(%) <sup>2</sup>	YIELD GMS /PLOT.	YIELD % OF NORQUAY.	HUNDRED KERNEL WEIGHT.
23-4X363-5	0.86	87.50	47.5	4.14	86.5	57.50	79.46	78.90	146.13	135.12	5.50
28-10X363-5	0.75	85.00	48.5	3.90	82.8	52.37	82.74	72.95	107.63	144.02	5.14
28-10X372-5	0.78	79.50	50.0	3.19	98.3	54.32	84.25	64.70	110.50	86.37	5.29
95-6X195-3	1.21	78.25	48.8	3.69	99.0	53.82	80.90	89.04	120.88	168.50	5.49
95-6X219-1	1.22	76.25	49.3	3.37	87.8	54.17	75.11	68.37	89.25	78.37	5.62
192-1X23-4	0.98	78.25	50.0	4.34	88.5	57.37	72.91	50.23	128.38	124.17	6.12
192-1X194-1	0.82	90.00	52.3	3.17	89.3	56.55	81.17	73.25	130.25	142.90	5.79
194-1X195-3	1.09	82.50	50.3	3.95	101.0	57.75	83.81	59.82	125.50	159.05	6.16
195-3X219-1	1.04	85.75	49.5	3.00	93.0	56.15	76.30	56.66	100.38	82.12	5.45
199-1X372-5	0.84	89.50	48.0	3.31	89.5	56.77	85.54	78.55	130.75	150.12	5.45
219-1X192-1	1.03	80.75	50.3	3.45	86.8	58.32	74.40	62.51	98.88	94.15	5.57
363-5X199-1	0.76	74.50	48.0	3.92	84.8	56.32	87.14	83.65	112.38	82.72	4.89
372-5X199-1	0.94	93.25	48.0	2.85	90.8	56.47	85.87	81.63	120.50	112.17	5.34
MEAN	0.95	83.15	49.3	3.56	90.6	55.99	80.73	70.78	119.10	119.99	5.52

<sup>1</sup>MEAN OF FOUR SAMPLES OF FORTY SEEDS.

<sup>2</sup>MEAN OF FOUR EARS OF EACH LINE.

TABLE 8. VALUES OF ELEVEN CHARACTERS (MEAN OVER FOUR REPLICATES) OF THE CONTROLS USED IN THE FIRST EXPERIMENT TOGETHER WITH MEAN VALUES FOR HYBRIDS AND INBREDS AND AN L.S.D. FOR COMPARISON OF ANY TWO LINES.

LINE NUMBER OR NAME.	CHARACTER										
	WEIGHT OF ORIGINAL SEED (gms): <sup>1</sup>	EMERGENCE (%)	DAYS TO HEADING.	FERTILE TILLERS /PLANT.	HEIGHT (cms).	FLORETS /HEAD.	OPEN-POLLINATED FERTILITY(%)	SELF-POLLINATED FERTILITY(%)	YIELD GMS. /PLOT.	YIELD % OF NORQUAY.	HUNDRED KERNEL WEIGHT.
GAZELLE	1.33	85.00	48.8	3.09	76.8	54.70	85.71	6.91	131.82	121.00	6.10
PROLIFIC	1.34	53.25	49.5	3.38	90.2	53.12	76.66	8.55	69.17	64.57	5.75
U.C.-85-41	1.53	65.75	54.5	2.62	65.8	70.82	81.17	-	105.00	92.31	6.91
NORQUAY	1.49	75.75	54.0	3.14	58.8	51.52	85.93	-	111.62	103.80	6.77
NEEFAWA	1.37	81.25	53.8	4.18	73.8	43.42	92.93	-	117.12	116.75	5.65
INBREDS (MEAN)	1.07	74.70	51.4	2.31	77.0	48.27	58.57	43.45	24.32	20.66	3.99
HYBRIDS (MEAN)	0.95	83.15	49.3	3.56	90.6	55.99	80.73	70.78	119.10	119.99	5.52
L.S.D. (.05)	0.109	5.159	1.282	0.736	12.127	3.078	6.986	18.956	22.174	37.722	0.408

<sup>1</sup>MEAN OF FOUR SAMPLES OF FORTY SEEDS.

<sup>2</sup>MEAN OF FOUR EARS OF EACH LINE.

pollination. Larger hybrid seed could possibly contribute to the improved growth of hybrids. Work has been done on the relationship between seed size, embryo size and heterosis in corn, but there are no consistent results that relate high embryo weight or large seed size to the level of heterosis (Whaley 1952). Whaley stated that there was some evidence in support of a hypothesis that there existed a relationship between early embryo development and heterosis although by seed maturity this has disappeared. In the results of the present experiment the mean weight of all inbred seed was 1.07 gm and that of the hybrids was significantly less ( $P = 0.01$ ), 0.95 gm. This compares with seed weights of the two out-pollinated varieties of 1.33 gm for Gazelle and 1.34 gm for Prolific. However, inbred and hybrid seed had come from plants grown in the glasshouse whereas the two varieties had previously been grown outside so comparison of these figures is invalid.

The reason for this difference in seed size between inbreds and hybrids can perhaps be explained by results of Briggie *et al.* (1964) working with wheat. They used two techniques when producing hybrid seed for heterosis tests in wheat, hand pollination, and a modification of the approach method. Only the latter method involved the cutting back of glumes and in each of two crosses the seed produced by this method was smaller than when glumes remained intact. It was suggested that exposure and resultant desiccation were responsible for the smaller seed. Hagberg (1953) also found that this problem occurred with barley when performing similar heterosis tests, he was able to overcome this by making intra-varietal crosses for selfed seed. The results of the present experiment seem to parallel these results in that emasculation involved cutting away much of the glumes whereas self-pollination did

not. This could account for the smaller seed size of the hybrids, although Kirk and Jones (1974) proposed that  $F_1$  hybrid seed of rye was small due to the influence of its weak, inbred, maternal parent. This could partially account for the small seed size but not why seed from crossing is smaller than seed from selfing, this is best explained by the adverse effect of the emasculation technique. A correlation analysis between the weight of hybrid seed and the seed weight of either female parent, mid-parent or best parent (Table 9) revealed a significant correlation ( $P = 0.05$ ) with the mid-parent value only. Assuming that seed size is related to the vigour of an inbred line, this indicates that there is no major effect of the vigour of the parental plant on the size of seed from artificial pollination.

Despite the smaller seed size, emergence of the hybrids was significantly better than that of the inbreds, emergence of the hybrids ranged from 74.5% to 93.2% and that of the inbreds from 57.0% to 86.2%. Emergence of Gazelle was 85.0%, slightly higher than the mean emergence of the hybrids but not significantly so, six of the hybrids had an emergence better than or equal to Gazelle. The emergence of Prolific the other control variety, was very poor, perhaps due to low quality seed, this resulted in a poor stand which might partially account for the low final yield of Prolific. From Appendix II it can be seen that neither within inbreds nor hybrids was emergence related to the size of seed sown.

Although heterosis was not reflected in larger hybrid seed, the second experiment carried out in the growth cabinet was performed to investigate the early growth of inbreds and hybrids and to determine if the hybrid advantage was expressed during these early stages of

TABLE 9. CORRELATION COEFFICIENTS BETWEEN HYBRIDS AND THEIR PARENTS  
FOR VARIOUS CHARACTERS.

CHARACTER	WITH MID-PARENTAL VALUE	WITH BEST PARENT VALUE		WITH FEMALE PARENT VALUE
WEIGHT OF ORIGINAL SEED	0.5265*	0.5069		0.3089
DAYS TO HEADING	0.5974*	(EARLIEST) 0.5286*	(LATEST) 0.5337*	0.4669
TILLERS PER PLANT	0.0068	0.0143		0.0302
FLORETS PER HEAD	0.3550	0.5746*		0.1472
HEIGHT	0.5273*	0.3570		0.1643
HUNDRED KERNEL WEIGHT	0.4332	0.3343		0.7492**
YIELD	0.0953	0.1702		0.3163
OUT-POLLINATED FERTILITY	0.0964	0.0323		0.0125
SELF FERTILITY	0.0005	0.2158		0.2829

\* = SIGNIFICANT AT .05 PROBABILITY.

\*\* = SIGNIFICANT AT .01 PROBABILITY.

growth. The results of this experiment are listed in Table 10. Similar studies of comparisons of hybrids and parents have been carried out by Kirk and Jones (1974) with rye, by Hagberg (1953) with barley and such studies with maize are mentioned by Whaley (1952).

The first measurement taken on the material, height eight days after planting, demonstrated that there was much variation in early growth among the inbred lines, from 4.9 cms to 10.5 cms with a mean of 9.69 cms. The hybrid lines showed less variation and had a mean height of 10.02 cms. Because of the high variation within inbred lines the difference between inbreds and hybrids did not prove significant. After 16 days, lengths of the first and second leaves were measured, length of the first leaf was again much more variable in the inbreds than in the hybrids. Again the mean for the inbreds of 11.67 cms was not significantly different from the mean for the hybrids of 12.33 cms. The mean length of the second leaf of the inbreds of 13.18 cms was significantly less ( $P = 0.05$ ) than the means for the hybrids of 17.06 cms. The differences between inbreds and hybrids in the lengths of both first and second leaves after 24 days of growth also proved to be significant ( $P = 0.05$  and  $P = 0.01$ , respectively).

After 38 days the plants were harvested, the width of the longest leaf of each plant was measured and the inbreds as a group had significantly narrower leaves ( $P = 0.01$ ) than the hybrids. For the inbreds the leaf width ranged from 0.33 to 0.51 cms with a mean of 0.42 cms, for the hybrids it ranged from 0.55 to 0.64 cms with a mean width of 0.58 cms. Although after 38 days the inbreds had a mean tiller number slightly less than that of the hybrids, 5.28 tillers per plant compared to 5.83 tillers per plant, this difference was not within the level of



TABLE 10. MEASUREMENTS TAKEN OVER A PERIOD OF 38 DAYS ON INBREDS AND HYBRIDS GROWN IN A CONTROLLED ENVIRONMENT, WITH F-VALUES FROM THE ANALYSIS OF VARIANCE OF THE TWO GROUPS.

LINE	CHARACTER									
	HEIGHT (cms) 8 DAYS. 16 DAYS.	FIRST LEAF LENGTH (cms) 16 DAYS.	SECOND LEAF LENGTH (cms) 16 DAYS.	FIRST LEAF LENGTH (cms) 24 DAYS.	SECOND LEAF LENGTH (cms) 24 DAYS.	LEAF WIDTH (cms) 38 DAYS.	TILLERS / PLANT 38 DAYS.	FRESH WEIGHT (gms) 38 DAYS.	DRY WEIGHT (gms) 38 DAYS.	
23-4	4.93	9.72	11.54	14.58	18.79	0.35	5.33	39.55	4.03	
95-6	6.26	11.26	8.42	16.41	18.65	0.33	5.50	45.97	3.65	
192-1	10.08	13.12	12.35	16.62	16.56	0.38	5.00	43.08	3.58	
194-1	10.47	12.89	18.50	20.78	27.41	0.45	5.75	49.57	3.98	
195-3	9.85	9.91	15.77	16.12	22.62	0.50	6.08	39.90	4.44	
199-1	9.80	13.13	14.95	20.03	24.97	0.51	4.92	47.40	4.83	
363-5	7.57	10.62	11.02	15.52	18.96	0.35	5.00	41.71	3.70	
372-5	10.54	12.69	12.89	16.09	22.22	0.42	4.67	44.33	4.32	
MEAN OF INBREDS.	8.69	11.67	13.18	17.02	21.27	0.42	5.28	43.94	4.06	
192-1X23-4	8.92	12.37	17.42	19.88	25.15	0.58	6.00	43.42	4.85	
194-1X195-3	10.61	12.27	17.57	19.80	27.17	0.55	5.83	46.02	4.56	
361-2X95-6	9.98	12.49	15.36	19.19	26.10	0.57	5.75	45.66	5.07	
363-5X199-1	9.63	11.65	17.42	21.79	26.32	0.57	5.20	48.37	4.96	
372-5X199-1	10.96	12.86	19.23	20.55	28.77	0.64	6.42	49.78	5.83	
MEAN OF HYBRIDS.	10.02	12.33	17.06	20.24	26.70	0.58	5.83	46.65	5.05	
F-VALUE	1.72	0.94	6.48*	9.37*	9.78**	28.67**	4.45	2.18	14.87**	

significance. Similarly the mean fresh weight of the inbreds was slightly less than that of the hybrids, 43.94 gm compared to 46.65 gm, but this also was not significantly different. Differences in dry weight between hybrids and inbreds, however, were significant ( $P = 0.01$ ). Dry weight of the inbreds ranged from 3.65 to 4.83 gm per plant with a mean of 4.06 gm, that of the hybrids from 4.56 to 5.83 gm with a mean of 5.05 gm per plant.

Kirk and Jones (1974) measured fresh weight of hybrid plants of rye and found that over a period of 60 days the hybrids had higher fresh weights than their inbred parents. They were able to attribute this to two factors, a faster rate of growth and also to some initial advantages in seed weight. This latter fact is not in agreement with the present study and can be attributed to the use of  $F_2$  rather than  $F_1$  seed by Kirk and Jones. Their study also indicated that in meristems, specifically root meristems, hybrids have almost twice as many cells per unit fresh weight as inbred lines. These results would seem to be in general agreement with the results of the present study, the hybrid advantage is expressed very early in the growth of hybrid rye. Both studies suggest that this advantage is not due to greater tillering of plants but to a faster growth rate of the plants. Early work by Bredeman and Heuser (1931) with intervarietal hybrids also established that in young plants increased dry matter was not dependent on increased tiller production.

The results of these experiments with rye are in agreement with those of maize workers, that the hybrid advantage becomes manifest in early post-germination growth, hybrid maize plants reaching maximum growth rates earlier than the inbreds (Whaley 1952). Whaley (1950)

reports finding significant differences in the growth of maize inbreds and hybrids as early as 10-12 days after germination, in the present study significant differences were found between rye inbreds and hybrids 16 days after planting. Hagberg (1953) measured three characters of inbred and hybrid barley. At four weeks growth there was no significant level of heterosis in either number of tillers, number of leaves on the first tiller or length of the second leaf. After seven weeks tillering of the hybrids was generally better than that of the inbreds but differences were still not significant, heterosis did not seem to be expressed in the early growth of this material. Perhaps it should be remembered that unlike maize or rye, barley is a naturally self-pollinating species and levels of heterosis relative to the parental lines could be expected to be less. It may also be of importance that Hagberg's experiment was carried out in the field whereas the experiments with rye and maize were carried out under controlled environments where variation within lines could be expected to be less.

On the evidence of this small experiment with rye and others with rye and maize it seems reasonable to assume that the hybrid advantage, at least in naturally out-breeding species, is in part a result of the more efficient early growth of the hybrids resulting in maximum growth rates being reached earlier. Whaley (1952) assumed this to be due to a more rapid unfolding of certain metabolic processes.

The more rapid growth of the hybrids was perhaps reflected in the time they required to reach heading in the field. Heading time of the inbreds varied from 48.8 to 54.5 days and of the hybrids from 47.5 to 52.3 days with means of 51.4 and 49.3 days, respectively. The hybrids were significantly ( $P = 0.01$ ) earlier than the inbreds but as a group

not significantly different from either Gazelle or Prolific which headed at 48.8 and 49.5 days, respectively. The non-rye controls U.C.85.41, Norquay and Neepawa were generally later heading than the ryes at 54.5, 54.0 and 53.8 days, respectively. All except one hybrid headed earlier than or equal to the earliest parent, one hybrid heading 3.2 days before its earliest parent. The length of period to heading proved to be significantly correlated with mid-parent ( $P = 0.05$ ) and also with either the earliest or latest parent (Table 9). The reason for this correlation with the parental values, as well as the mid-parental value, is probably due to the crossing procedure. As already mentioned, lines were crossed which were heading at the same time (except towards the end of the crossing period when some late tillers of early lines were used as a pollen source for late lines) and as a result the two parental values were relatively similar and close to the mid-parental value. As the mid-parental value shows a correlation with the hybrid value, so do the parental values.

Neither Müntzing (1943) nor Lundquist (1966) investigated heading in their experiments with rye although Kuznecov (1950) found that inter-varietal rye hybrids headed earlier than the pure lines. Fonesca and Patterson (1967) found the same situation in wheat hybrids, and Hagberg (1953) and McNeal *et al.* (1965) found that barley and wheat hybrids generally headed intermediately to their parents or as early as the earliest parent. The significant correlation between the hybrid and mid-parental values obtained in the present study would perhaps suggest that heading date of the material is controlled mainly by additive rather than dominant gene effects.

The number of fertile tillers of the hybrids was significantly

greater than that of the inbreds ( $P = 0.01$ ), the hybrids had from 2.85 to 4.34 tillers per plant with a mean of 3.56 and the inbreds 1.67 to 2.87 tillers with a mean of 2.31. Gazelle and Prolific had 3.09 and 3.88 tillers per plant respectively, the hybrids as a group did not have significantly more tillers than Gazelle. Lundquist (1966) also found that hybrids tillered much better than inbreds although levels of tillering were not above that of the control out-pollinated population. The correlation between level of tillering and final yield, although high was not significant among either inbreds or hybrids (Appendix II). It may be of significance that in both inbreds and hybrids the level of tillering showed a negative correlation with emergence, this perhaps suggests that some variation in tillering was due to different stand densities. This could also be the case with Prolific which had a reduced stand due to poor emergence and showed profuse tillering. The level of tillering of the hybrids showed no correlation with either mid-parent or best-parent values, perhaps because of the variation introduced through different stand densities. Inspection of the results of Lundquist (1966) also shows no relationship between the tillering of the hybrid and that of its parents. In his material only one hybrid out of seventy tillered more than the outbred population whereas in the present experiment all except one tillered more than Gazelle. This could reflect the relatedness of the lines used by Lundquist limiting the level of heterosis, or also the genetic background of the lines or control used in the present experiment.

Like corn, rye is characterized by becoming shorter on inbreeding and returning to normal height (or more) on hybridization. In the present experiment the inbred lines had a mean height of 77.0 cms, ranging

from 49.3 cms to 93.8 cms, whereas the hybrids had a mean height of 90.6 cms, ranging from 82.8 to 101.0 cms. There were significant differences in height among the inbred lines ( $P = 0.01$ ) but not among the hybrids, inbreds were also significantly shorter than hybrids ( $P = 0.01$ ). Gazelle and Prolific had mean heights of 76.8 and 90.3 cms and the hybrids as a group were significantly taller than Gazelle. No source populations were available to relate the height of the inbreds or hybrids to, but Müntzing (1943) and Lundquist (1966) both found decreases in height of about 20% after 17 and 25 generations, respectively. Müntzing found that  $F_1$  hybrids were more variable than a sample of plants from the population but had the same mean height, the hybrids produced by Lundquist were on average about 8% higher than the source population. In the present experiment hybrids were approximately 15% taller than the inbreds, about the same height as the variety Prolific. Gazelle was much shorter than Prolific, in fact, equal to the mean height of the inbreds. The height of the hybrid lines, like days to heading, was significantly correlated with the mid-parental value suggesting that this character also was controlled by mainly additive gene effects.

Height of the inbreds was significantly correlated ( $P = 0.05$ ) with their final yield and highly correlated with original seed weight and open-pollinated fertility (see Appendix II). This was probably due to the fact that these four characters are affected by inbreeding to similar degrees and that the more sensitive inbred lines were depressed in all four characters while vigorous inbred lines were not. Head size, as measured by the number of florets per head, was also significantly correlated with height and highly correlated with the yield of

the inbred lines. Hybrids had significantly more florets per head than inbreds ( $P = 0.01$ ) a mean of 48.3 compared to 55.9, but did not have significantly larger heads than Gazelle which had 54.7 florets per head. Prolific also had relatively large heads (53.1 florets). In the present experiment the number of florets per head of the hybrids showed a significant correlation with the better parent (Table 9). This would perhaps suggest that head size is controlled by mainly dominant gene effects.

Fertility, as measured by seed-set under open-pollination, ranged from 42.8% to 78.6% for inbreds and from 72.9% to 87.1% for hybrids, mean fertility of the inbreds was 58.6% and of the hybrids 80.7%, significantly greater ( $P = 0.01$ ) than the inbreds. The fertility of the hybrids was slightly lower than that of Gazelle (85.7%) but not significantly so, the fertility of Prolific was 76.7%. These results are in good agreement with those of Müntzing (1943) who found fertilities of 59%, 78% and 83% for inbreds, hybrids and the outcrossed population, respectively. They also agree quite closely with the results of Lundquist (1966) who found fertilities (of the longest head) of 67%, 86%, and 85% in his material. In the present study there seemed to be no relationship between the fertility of the hybrids and that of the inbred parents (Table 9). Amongst the inbreds open-pollinated fertility was significantly correlated with yield; amongst the hybrids there was no such correlation although it is interesting that fertility was negatively correlated with original seed weight and also with one hundred kernel weight. This would suggest that in the hybrid material the high fertility may have been limiting seed size to a certain extent.

Self-fertility of the hybrids was also significantly higher than

that of the inbreds ( $P = 0.01$ ), inbreds had a mean fertility of 43.5% and hybrids 70.8%. Gazelle and Prolific, having undergone no selection for self-fertility were almost completely sterile having fertilities of 6.9% and 8.5%, respectively. Among the inbreds there was a highly significant ( $P = 0.01$ ) correlation between self-fertility and open-pollinated fertility. This calculation was performed without line 199-1 as in the field the bagged heads of this line set no seed whereas the line had previously been about 50% fertile in the glasshouse. This correlation would suggest that the self-sterility mechanism has been lost completely from the sterile lines, sterility under either self- or cross-pollinating conditions being due to purely physiological causes perhaps related to the vigour of the line. The lowered fertility when selfed could be due to detrimental effects of the bagging procedure on the environment surrounding the head.

Amongst the hybrid lines there was no correlation between self- and cross-pollinated fertility. Correlation analysis between hybrids and parents, carried out exclusive of line 199-1 or crosses involving it, also revealed no relationship between the self-fertility of the parents and that of the hybrids (Table 9). Müntzing (1943) also investigated self-fertility in hybrids and population plants. Open pollinated hybrids had self-fertilities of from 49.0% to 77.2% with a mean value of 62.9%; bagged hybrids were more variable ranging from 48.6% to 93.1% with a mean of 68.0%, as expected population plants were very sterile ranging from 0.0% to 12.8% self-fertile. These results are not in agreement with those of the present experiment in that fertility under bagging is higher than fertility under open-pollinated conditions. This could possibly be due to environmental differences between the two



experiments or differences in technique.

The genetic basis of self-incompatibility in rye was first outlined by Lundquist (1956) based on two multiple-allelic incompatibility loci. Further investigations utilizing outbred populations and inbred lines led Lundquist (1958) to conclude that mutation of these loci was responsible for the origin of self-compatibility in inbred lines. After further study (Lundquist 1960 and 1968) he concluded that the incompatibility loci had a bipartite or even more complex structure, the unbalanced recombination of which led to loss of self-incompatibility. However, his results also led him to conclude that there existed an additional major gene unrelated to the incompatibility loci, independently inherited and able to turn into a self-fertility determinant. Wricke (1969) also studied the inheritance of self-fertility in rye. He concluded that self-fertility is not caused by an allele of one of the incompatibility loci but by a third factor which could possibly interact with these loci. In the present study no conclusions can be made on the self-fertility mechanism, such minor differences as were present between inbred lines were assumed by Wricke (1969) to be controlled by sub-vital (minor) genes.

One hundred kernel weight of the hybrids was significantly higher than that of the inbreds ( $P = 0.01$ ). The inbred lines had one hundred kernel weights ranging from 2.67 gm to 4.92 gm with a mean of 3.99 gm, and the hybrids ranged from 4.89 gm to 6.16 gm with a mean of 5.52 gm. Gazelle and Prolific had one hundred kernel weights of 6.10 gm and 5.75 gm, the seed of the hybrids as a group was significantly smaller than that of Gazelle ( $P = 0.01$ ) although two of the three highest yielding hybrids had seed as large as Gazelle. This difference between

the hybrids and Gazelle could be due to the large seed of Gazelle which was also much bigger than that of Prolific. It is also possible that the introduced lines from which the inbreds and ultimately the hybrids were obtained had small seed size. One hundred kernel weight of the hybrids was significantly correlated ( $P = 0.01$ ) with that of the female parent indicating strong maternal (cytoplasmic) control of this character (Table 9). Amongst the inbreds one hundred kernel weight was significantly correlated ( $P = 0.05$ ) with three other characters, the weight of the original seed, days to heading and yield. No significant correlations existed among the hybrids although a high correlation was shown with days to head and a relatively high negative correlation was shown with open-pollinated fertility as mentioned previously. This latter point would suggest an interaction between seed size and fertility.

Lundquist (1966) found that the mean yield of inbred lines was 2.86 gm, of hybrids 11.08 gm, and of double-cross hybrids 11.40 gm. These yields did not approach that of the outbred source population of 16.67 gm (per plot). The best  $F_1$  hybrid yielded only 15.3 gm and one exceptional double-cross hybrid yielded 20.36 gm. Previously, Müntzing (1943) had found that hybrids outyielded the outbred population, but this was on a per plant basis and hybrid plants were less dense than the population plants due to winter kill. In the present study inbreds and hybrids gave yields equivalent to the inbreds and hybrids of Lundquist (1966). The mean yield of the inbred lines was 24.3 gm per plot, there was a wide range in yield from 9.4 to 59.8 gm per plot. The hybrids had a mean yield of 119.1 gm, ranging from 89.2 to 152.5 gm per plot significantly higher than the inbreds ( $P = 0.01$ ). Gazelle and Prolific had yields of 131.8 gm and 69.1 gm per plot, respectively,

the low yield of Prolific could be partially due to the poor stand as previously mentioned. The yield of the hybrids as a group was not significantly different from that of Gazelle although three hybrids were almost equal in yield to Gazelle and two, 23-4 x 363-5 and 194-1 x 195-3 yielded 11.5% and 16.0% above it.

Correlation analysis of the relationship between yield of hybrids and yield of the inbred parents (Table 9) did not reveal any significant relationships. The highest correlation was obtained between hybrids and the female parent ( $r = 0.3163$ ), both best parent and mid-parent correlation value were very low. This high correlation could be due to the significant correlation between one-hundred kernel weight of the hybrids and that of the maternal parent assuming that one hundred kernel weight is a major component of yield. From these results prediction of the yield of a hybrid from that of its parents does not seem possible, selection of a female parent with high one-hundred kernel weight would seem most advantageous.

Amongst the hybrids relatively high but insignificant correlations were found between yield and emergence and yield and tillers per plant. This would suggest that a significant yield component of the hybrids was the number of fertile tillers per plot. In fact the number of tillers per plot was measured originally. It was presented in the results as the number of tillers per plant as it was thought this would be more meaningful. The number of tillers per plot of the hybrids was found to be significantly correlated with the yield of the hybrids ( $P = 0.01$ ,  $r = 0.7445$ ). Tillers per plot was mainly a function of the number of tillers per plant ( $r = 0.7594$ ) but also of emergence. As noted before, tillers per plant was negatively correlated with emergence

so it can be assumed that low emergence resulted in less competition and a greater average number of tillers per plant. However, the increase in tillers per plant did not make up for the fewer plants and as a result tillers per plot was correlated with emergence (but not significantly so) with a value of  $r = 0.4713$ .

Close inspection of Table 7 reveals that there are two cases where two inbred lines are both involved with two other lines, these are shown in Table 11. From crosses involving the four lines 363-5, 372-5, 199-1 and 28-10 it can be seen that a combination of high yielding inbreds gives a high yielding hybrid, of lower yielding inbreds a low yielding hybrid, and that a combination of low and high yielding inbreds results in a hybrid of intermediate yield. In the other case, with lines 192-1, 195-3, 194-1, and 192-1 this pattern is not so clear cut. Line 194-1 was a higher yielding inbred than 219-1 and gave higher yielding hybrids than 219-1 when crossed with lines 192-1 and 195-3. However, line 192-1 was higher yielding than line 195-3 but gave lower yielding hybrids than 195-3 with lines 194-1 and 192-1. These results would suggest that at least in certain combinations the yielding ability of the hybrid is dependent on that of both parental inbred lines although we have seen that this does not hold for the results as a whole.

As mentioned earlier, plots of Norquay wheat were included regularly throughout the field trial with two purposes in mind. The first was that the wheat would equalize competition effects between plots, and also be effective in separating rye plots should lodging occur. However, lodging did not occur because of the very dry conditions in 1974 which probably reduced both height and tillering of the material. The second purpose of the Norquay plots was purely investi-

TABLE 11. THE YIELD OF CERTAIN HYBRID LINES IN RELATION TO  
THE YIELD OF THEIR PARENTS.

LINE NO.	HIGH YIELDING PARENT	LOW YIELDING PARENT
	372-5	363-5
HIGH YIELDING 199-1 PARENT	130 gms.	112 gms.
LOW YIELDING 28-10 PARENT	110 gms.	107 gms.
LINE NO.	HIGH YIELDING PARENT	LOW YIELDING PARENT
	192-1	195-3
HIGH YIELDING 194-1 PARENT	130 gms.	152 gms.
LOW YIELDING 219-1 PARENT	98 gms.	100 gms.

gative, to see if they could be used to adjust the yield of the experimental plots and bring about a reduction in error due to soil variability. Norquay is, of course, a wheat whereas most of the field experiment was rye. It seems unlikely that the fertility requirements of a wheat are the same as those of rye; rye is known to be much better adapted to low fertility conditions and also rye is much more tolerant of droughting than wheat. The analysis of variance of the adjusted treatment means (as a percentage of the mean of two adjacent Norquay plots) resulted in an error term of 721, nearly three times higher than that of the analysis of variance of actual yield, 248. In all cases except one the F values obtained from the analysis of variance of adjusted means were much lower than those obtained from that with actual means (Appendix I). These results would suggest that the use of Norquay to take into account soil variability was not successful and was of no advantage. The main reason for this has already been outlined, the two species do have different fertility requirements and so one species cannot be used to give a measure of soil fertility for another species. Also, since 1974 was a very dry year and observations in the field confirm that rye is much more tolerant to droughting than wheat, low wheat yields of wheat partially due to droughting were not paralleled by low rye yields. The technique of using adjacent plots to adjust yields would seem to require a variety of the same species. In the present experiment Gazelle would have been used but this would have negated the primary purpose of the adjacent plots which was to allow separation of experimental plots had lodging occurred, however, this did not happen and inclusion of Gazelle as adjacent plots could have been very valuable and might have increased the accuracy of the experiment.

## 5. CONCLUSIONS AND RECOMMENDATIONS

This experiment was undertaken with the aim of attempting to obtain some measure of the level of heterosis expressed in  $F_1$  rye hybrids produced by crossing inbred lines. The basis on which the feasibility of hybrid rye ultimately depends is the yield of the hybrids relative to the best adapted out-pollinating varieties that might be produced. In the present study the hybrids as a group did not yield significantly higher than Gazelle, the best adapted variety, however certain hybrids were superior to Gazelle yielding up to 16% more. In evaluating these results a number of points must be taken into consideration. Firstly, the selection of the inbred lines was purely random, no tests had been carried out prior to the experiment to test for either specific or general combining ability. Secondly, most of the lines used had been derived from unadapted introduced varieties and it seems unlikely that any conscious selection for adapted high-yielding lines had been practiced. Thirdly, these results are based on a minimum of material, only eleven lines were utilized and the hybrids represent only thirteen cross-combinations. When these three points are taken into consideration the results obviously warrant further testing of hybrid rye utilizing high-yielding adapted inbred lines previously selected on the basis of combining ability.

It was perhaps unfortunate that the genetic potential of the inbred lines was confounded by their unknown level of inbreeding. If all the lines had been equally inbred their potential and the parental-hybrid relationships might have been clearer. This could have allowed more conclusions to have been drawn on the choice of parents required to

produce a good hybrid. In the present experiment very little information was obtained on the characteristics desired of inbred lines in order to produce a good  $F_1$  hybrid. Yield of hybrid lines was correlated with neither mid-parent nor best-parent yield, however, there was some evidence that the higher yielding inbreds tended to produce higher yielding hybrids. Hybrid yields did show a low correlation with the yield of the maternal parent and it seems likely that this was due to significant maternal effects on seed size.

Hybrid advantage was shown to be due to more rapid early growth of the hybrids and this factor is likely to have been in part responsible for a number of the differences between hybrids and inbreds. Hybrids headed earlier than inbreds, they had more fertile tillers per plant, were taller, had larger heads with larger seed and had both better cross- and self-fertility than inbreds.

In the future, it would seem advisable to carry out some experiments on combining ability between inbred lines and to establish a large number of lines for this purpose. Producing hybrid seed by artificial crossing techniques is a limiting factor when testing for heterosis but hopefully small initial tests on combining ability will allow selection of only the most desirable lines. For large-scale production of rye hybrids it seems likely that cytoplasmic male-sterility and the necessary restorer genes could be incorporated into the desired inbred lines. Work on these procedures is now underway.



## LITERATURE CITED

- ALLARD, R. W. 1966. Principles of plant breeding. John Wiley and Sons, Inc., New York. p. 485.
- BAEVA, R. 1962. (The use of intervarietal mixtures of rye, a method of increasing yield). *Izv. naučn.-izsled. Inst. Rasten. Sofija*. 15: 51-62. (P.B.A. 33: 3035).
- BARTNIK, J. 1965. The nutritive value of rye as compared to wheat. Part I. The content of nutrients of wheat and rye grains on the background of their "availability" and biological value. *Panstw. Zaklad. higien* 16: 233-241. (cited by Haerberle 1974).
- BAUER, F. 1968. Heteróizhatas-vizsgálatok rozsnál szabadmegporzás esetén. (Investigations on the heterosis effect in open-pollinated rye). *Duna-Tisza k. mezőgazd. Kísérlet. Int. Bull. Kecskemet* 3: 33-41. (P.B.A. 39: 4535).
- BOROJEVIĆ, S. 1959. Analiza ukrštanja tetraploidnih sorti raži. (An analysis of crosses of tetraploid rye varieties). *Savremen. Poljopr., Novi Sad* 1959, 7: 116-120. (P.B.A. 37: 3280).
- BREDEMAN, G. and W. HEUSER. 1931. Beiträge zur Heterosis bei Roggen. (Notes on heterosis in rye). *Z. Zuchtung* 16: 1-56 (P.B.A. 1: 345).
- BRIGGLE, L. W., R. J. DAUM and H. STEVENS. 1964. Expression of heterosis in two wheat crosses. *Crop Sci.* 4: 220-223.
- BRIGGS, F. N. and P. F. KNOWLES. 1967. Introduction to plant breeding. Reinhold Publishing Corporation, New York. p. 426.
- CANADA GRAINS COUNCIL. 1974. A summary of the findings and recommendations of the working group on energy grains. September 1974. p. 13.
- CANDLISH, E. 1975. Computer evaluation of inclusion of rye as an ingredient in a laying-hen diet and in a fattening swine diet. Personal communication.
- CARMICHAEL, J. S. and M. W. NORMAN. 1970. Rye production in Canada. *Can. Farm Econ.* 5: 17-21.
- CHERNICK, S. S., S. LEPKOVSKY and I. CHAIKOFF. 1948. A dietary factor regulating the enzyme content of the pancreas. *Amer. J. Physiol.* 155: 33-41.

- CRAMPTON, E. W. 1933. The comparative feeding value for livestock of barley, oats, wheat, rye and corn. National Research Council report No. 28, p. 107.
- CROW, J. F. 1952. Dominance and overdominance. In "Heterosis", Ed. by John W. Gowen. Iowa State College Press, Ames, Iowa.
- DAVENPORT, C. B. 1908. Degeneration, albinism and inbreeding. *Science* 28: 454-455.
- EAST, E. M. 1908. Inbreeding in corn. Rept. Connecticut Agric. Expt. Sta. for 1907: 419-428.
- EGGUM, B. O. 1968. Aminosyrekoncentration og proteinkvalitet. Stourgards Forlag, Copenhagen. p. 90.
- EWART, J. A. D. 1967. Amino acid analyses of cereal flour proteins. *J. Sci. Fd. Agric.* 18: 548-552.
- F.A.O. 1965. Trends and patterns in the world rye economy. *Monthly Bulletin of Agric. Econ. and Stats.* 14: 2-13.
- FERNANDEZ, R., E. LUCAS and J. MCGINNIS. 1974. Comparative nutritional value of different cereal grains as protein sources in a modified chick bioassay. *Poultry Science* 53: 39-46.
- FERWERDA, F. P. 1951. Inteelt en Heterosis bij rogge. (Inbreeding and heterosis in rye). *Landbouwkundig Tijdschrift* 63(5): 319-330.
- FONESCA, S. and L. PATTERSON. 1967. Hybrid vigour in a seven-parent diallel cross in common winter wheat. *Crop Sci.* 8: 85-88.
- FRIEND, D. W. 1970. Comparison of some milling products of barley and rye when fed in diets to rats. *Can. J. Animal Science* 50: 345-348.
- FRIMMEL, F. 1939. Beitrag zur Xenienfrage bei Roggen. (A note on the question of Xenia in rye). *Züchter* 11: 301-307. (P.B.A. 10: 420).
- FRUWIRTH, C. 1913. Geschlechtliche Mischung von Roggenformenkreisen. *Zeitschrift für Pflanzenzüchtung* 1: 504-507.
- GASPAR, I. 1973. (A conference on the study and use of heterosis in rye, Leningrad 1973). *Probleme Agricole* 25(11): 72-75. (P.B.A. 44: 3099).
- GEIGER, H. H. 1971. Cytoplasmatisch-genische Pollensterilität in Roggenformen iranischer Abstammung. (Cytoplasmic-genic pollen sterility in rye forms of Iranian derivation). *Naturwissenschaften* 58: 98-99. (P.B.A. 41: 7377).

- GEIGER, H. H. 1972. Wiederherstellung der Pollenfertilität in cytoplasmatisch männlich sterilem Roggen. (Restoration of pollen fertility to cytoplasmic male sterile rye). *Theor. Appl. Genetics* 42: 32-33.
- \_\_\_\_\_ and F. W. SCHNELL. 1970a. Cytoplasmic male sterility in rye. *Crop Sci.* 10: 590-593.
- \_\_\_\_\_. 1970b. Die Züchtung von Roggensorten aus Inzuchtlinien. I. Selbstungsanteile in Polycross-Nachkommenschaften. (Breeding rye varieties from inbred lines. I. Selfing-proportions in Polycross Progenies). *Theor. Appl. Genetics* 40: 305-311.
- GLUSCENKO, I. E. 1941. (Results of twice repeated cross-pollination of rye in the plants of the collection). *Jarovizacija* 1(34): 27-33. (P.B.A. 12: 137).
- HAEBERLE, B. G. 1974. Mode of inheritance and nutritional significance of the 5-n-Alkylresorcinols of rye (*Secale cereale* L.) Masters Thesis. University of Manitoba.
- HAGBERG, A. 1952. Heterosis in some crosses between populations of rye and red clover. *Hereditas* 38: 506-570.
- \_\_\_\_\_. 1953. Heterosis in Barley. *Ibid.* 39: 325-348.
- HALPIN, J. G., C. E. HOLMES and E. B. HART. 1936. Rye as a feed for poultry. *Poultry Science* 15: 3-8.
- HELBAEK, H. 1971. The origin and migration of rye, *Secale cereale* L.; a palaeo-ethnobotanical study. In "Plant life of Southwest Asia", 265-280. Botanical society of Edinburgh, Aberdeen, Scotland.
- HEUSER, W. 1935. Abschliessende Versuche zum Problem des Maultierroggen. (Concluding experiments on the problem of Maultierroggen). *Landw. Jb.* 81: 577-583. (P.B.A. 6: 527).
- HORSLEY, B. 1969. Rye - A casualty of our affluent society. *Foreign Agriculture* VII(12): 2-4.
- HUANG, R. C. and J. BONNER. 1962. Histone, a suppressor of chromosomal RNA synthesis. *Proc. Nat. Acad. Sci.* 18: 1216-1222.
- HUNGATE, R. E. 1966. The rumen and its microbes. Academic Press, New York, p. 533.
- JANICKI, J. and KOWALCZYK. 1967. Der ernährungs-physiologische Wert des Roggens und Weizens mit specieller Berücksichtigung des Eiweisses und der Vitamine. *Getreide und Mehl* 17: 73-77. (cited by Munck 1972).

- KHUSH, G. S. 1963. Cytogenetic and evolutionary studies in *Secale*. III. Cytogenetics of weedy ryes and the origin of cultivated rye. *Economic Botany* 17: 60-71.
- KIHLBERG, R. and L. E. ERICSON. 1964. Amino acid composition of rye flour and the influence of Amino acid supplementation of rye flour and bread on growth, nitrogen efficiency ratio and liver fat in the growing rat. *J. Nutrition* 82: 385-394.
- KIRK, D. J. and R. N. JONES. 1974. Quantitative nuclear variation in inbred lines and hybrid rye. *Heterdity* 32(3): 357-363.
- KNIERIEM, W. von. 1900. Der Roggen als Kraftfuttermittel. *Landwirt. Jahrb.* 29: 483-523. (cited by Munck 1972).
- KOBYLYANSKII, V. D. 1968. (The uses of heterosis in diploid rye). *Bjull. vses. Inst. Rasten, Vavilov.* 13: 33-37. (P.B.A. 39: 4536.
- \_\_\_\_\_ and Yu. A. KOSOV. 1971. (Heterosis in hybrids of winter rye in Leningrad province). *Byulleten Vsesoyuznogo Ordena Lenina Instituta Rastenievodstva Imeni N.I. Vavilova* 20: 24-48. (P.B.A. 42: 7481).
- \_\_\_\_\_ and A. G. KATEROVA. 1973. (Inheritance of cytoplasmic and nuclear male sterility in diploid winter rye). *Genetika* 9(7): 5-11.
- KOFRÁNYI, E. and H. MÜLLER-WECKER. 1960. Zur Bestimmung der biologischen Wertigkeit von Nahrungsproteinen. IV. Der Vergleich der Wertigkeiten von Milch-, Roggen- und Weizenweiss mit Vollei und ihre Berechenbarkeit aus der Bausteinanalyse. *Ztschr. Physiol. Chem.* 320: 233. (cited by Kihlberg and Ericson 1964).
- KOSOV, Ju. A. 1969. (A study of heterosis in rye). *Sborn. Trud. Aspirant. Molod. nauč. Sotrud. vses. nauč.-issled. Inst. Rasten.* 10: 126-132. (P.B.A. 40: 668).
- \_\_\_\_\_. 1970. (Influence of hybridization on the manifestation of heterosis in winter rye). *Ibid.* 15: 124-130. (P.B.A. 41: 924).
- KOZYRJ, A. T. 1950. (The economic and biological properties of the hybrids of rye). *Selekcija i Semenovodstvo* 11: 27-29. (P.B.A. 22: 324).
- KRASNIUK, A. A. 1941. (Twelve years inbreeding in rye). *Socialistic Grain Farming, Saratov.* 2: 26-46. (P.B.A. 12: 450).
- \_\_\_\_\_. 1946. (Breeding rye by the method of composite populations). *Agrobiologija* 2: 44-51. (P.B.A. 17: 1632).

- KUZNECOV, V. S. 1950. (Sowing winter rye with cross-pollinated seed). *Sovetskaja Agronomija* 8: 89-92. (P.B.A. 21: 997).
- LAPINSKI, M. 1972. Cytoplasmic-genic type of male sterility in *Secale montanum* Guss. *Wheat Inf. Serv.* 35: 25-28.
- LEITH, B. D. and H. L. SHANDS. 1938. Fertility as a factor in rye improvement. *J. Amer. Soc. Agron.* 30: 406-418. (P.B.A. 8: 1524).
- LEVIN, D. A. 1971. Plant phenolics: An ecological perspective. *American Naturalist* 105: 157-181.
- LUNDQUIST, A. 1956. Self incompatibility in rye. I. Genetic control in the diploid. *Hereditas* 42: 293-348.
- \_\_\_\_\_. 1958. Self incompatibility in rye. IV. Factors related to self-seeding. *Ibid.* 44: 193-256.
- \_\_\_\_\_. 1960. The origin of self-compatibility in rye. *Ibid.* 46: 1-19.
- \_\_\_\_\_. 1966. Heterosis and inbreeding depression in auto-tetraploid rye. *Ibid.* 56: 317-366.
- \_\_\_\_\_. 1968. The mode of origin of self-fertility in Grasses. *Ibid.* 59: 413-426.
- MacAULIFFE, T. and J. MCGINNIS. 1971. Effect of antibiotic supplements to diets containing rye on chick growth. *Poultry Science* 50: 1130-1134.
- MAYER, H. K. H. A. 1944. Iets over inteelt-proefnemingen bij ragge. (On inbreeding experiments with rye). *Studiekring voor Plantenveredeling, Wageningen.* 44(4): 15-18. (P.B.A. 18: 1564).
- McNEAL, F. H., D. E. BALDRIDGE, M. A. BERG and C. A. WATSON. 1965. Evaluation of three hard red spring wheat crosses for heterosis. *Crop Sci.* 5: 399-400.
- MINJA, L. 1970. Nutritive value of rye. Masters Thesis, University of Saskatchewan.
- MEDVEDEV, P. F. 1950. (The productiveness of winter rye varieties obtained by intervarietal open-pollination). *Selekcija i Semenovodstvo* 12: 9-13. (P.B.A. 22: 2643).
- MORAN, E. T. Jr. and J. MCGINNIS. 1965. The effect of cereal grain and energy level of the diet on the response of turkey poults to enzyme and antibiotic supplements. *Poultry Science* 44: 1253-1261.

- MORAN, E. T. Jr., S. P. LALL and J. D. SUMMERS. 1969. The feeding value of rye for the growing chick: Effect of enzyme supplements, antibiotics, autoclaving and geographical area of production. *Ibid.* 48: 939-949.
- MUNCK, L. 1972. Improvement of the nutritional value in cereals. *Hereditas* 72: 1-128.
- MÜNTZING, A. 1943. Double crosses of inbred rye. *Botanika Notiser*, Lund 1943, pp. 333-345.
- \_\_\_\_\_. 1954. An analysis of hybrid vigour in tetraploid rye. *Hereditas* 40: 265-277.
- NILSSON, N. H. 1921. Selective Verschiebung der Gametenfrequenz in einer kreuzungspopulation von Roggen. *Ibid.* 2: 364-369.
- \_\_\_\_\_. 1937. Eine Prüfung der Wege und Theorien der inzucht. (A test of methods and theories of inbreeding). *Ibid.* 23: 236-256. (P.B.A. 7: 1239).
- PETERSON, R. F. 1934. Improvement of rye through inbreeding. *Scientific Agriculture* 14: 651-668.
- PFÄHLER, P. L. 1966a. Heterosis and homeostasis in rye (*Secale cereale* L.). I. Individual plant production of varieties and intervarietal crosses. *Crop Sci.* 6: 397-400.
- \_\_\_\_\_. 1966b. II. Production of varieties, intervarietal crosses and composite populations under various population densities. *Ibid.* 6: 401-405.
- PIVNENKO, M. Ja. 1963. (Efficacy of heterosis in winter rye). *Visn. sil's'kogosp. Nauk* (News Agric. Sci.) 6: 41-45. (P.B.A. 36: 1806).
- POLANOWSKI, A. 1967. Trypsin inhibitor from rye seeds. *Acta Biochimica Polonica* 14: 387-395.
- POLYANKOVA, T. F., S. I. NARBUT and O. P. NALIMOV. 1971. The content of DNA and basic proteins in plant sperm of garden radish inbred lines. *Cytol. genet.* 5: 161-170. (cited by Kirk and Jones 1974).
- PREECE, I. A. and K. G. MACKENZIE. 1952. Non-starchy polysaccharides of cereal grains. II. Distribution of water-soluble gum-like materials in cereals. *J. Inst. Brew.* 58: 457-464.
- PRINCIPLES AND PRACTICES OF COMMERCIAL FARMING 1974. Published by The Faculty of Agriculture, The University of Manitoba.

- PRJANISNIKOVA, Z. D. 1939. (The question of utilizing the products of inbreeding in rye breeding). *Selekcija i Semenovodstvo* 6: 15-16. (P.B.A. 10: 418).
- PUTT, E. D. 1954. Cytogenetic studies of sterility in rye. *Can. J. Agric. Sci.* 34: 81-119.
- RÉDEI, Gy., E. VÁRÓCZY and REDEI, Gy. 1954. A rozs állománykeresztesek kérdésének kísérletes vizsgálata. (Experimental investigations on the problem of crossing rye populations). *Növénytermelés* 3: 181-202. (P.B.A. 26: 2271).
- REEVES, D. L. 1971. Do you have a rye future ahead? *Crops and Soils* 22: 15-17 (April to May).
- RÜMKER, K. von and R. LEIDNER. 1914. Ein Beitrag zur Frage der Inzucht bei Roggen. (A note on the question of inbreeding in rye). *Zeitschrift für Pflanzenzüchtung* 2: 427-444.
- SALIMEN, M. 1959. Heterosi-ilmiö rukilla. (The phenomenon of heterosis in rye). *Koetoiminta ja Käytäntö* 16: p. 27. (P.B.A. 30: 3845).
- SCHABEN, L. J. 1948. Rye, a source of daily bread. *Foreign Agriculture* 12: 163-168.
- SCHRIBAU, . 1931. L'amélioration du seigle. (Rye improvement). *C.R. Acad. Agric. Fr.* 17: 561-592. (P.B.A. 1: 519).
- ŠESTAKOV, V. E. and V. A. ORLOV. 1957. (Methods of obtaining hybrid rye seed and studying its productiveness). *Agrobiologija* 2: 40-43. (P.B.A. 28: 1597).
- SHULL, G. H. 1908. The composition of a field of maize. *Rept. Amer. Breeders' Assoc.* 4: 296-301.
- \_\_\_\_\_ . 1952. Beginnings of the heterosis concept. *In* "Heterosis", Ed. by John W. Gowen. Iowa State College Press, Ames, Iowa.
- SLABOŃSKI, A. 1964. Primary research on heterosis in tetraploid rye. *Genet. Polon.* 5: 130-131. (P.B.A. 36: 387).
- SNEDECOR, G. W. and W. G. COCHRAN. 1973. Statistical Methods. Iowa State University Press, Ames, Iowa. p. 593.
- STEGLICH, R. and H. PIEPER. 1922. Verebungs-und Züchtungsversuche mit Roggen. *Fühlings Landw. Zeitung* 71: 201-222.
- STRICKBERGER, M. W. 1972. Genetics. MacMillan, New York. p. 868.

- STRØMNAES, A. S. and B. M. KENNEDY. 1957. Effect of baking on the nutritive value of proteins in rye-bread with and without supplements of non-fat dry milk and of lysine. *Cereal Chem.* 34: 196-200.
- STUTZ, H. C. 1972. On the origin of cultivated rye. *Amer. J. Bot.* 59(1): 59-70.
- SYBENGA, J. 1958. Inbreeding effects in rye. *Zeitschr. F. Vererbungsllehre* 89: 338-354.
- U.S.D.A. 1971. Supplement to food grain statistics. *Statistical bulletin* 423.
- VAN HEEMERT, C. and J. SYBENGA. 1972. Identification of the three chromosomes involved in the translocations which structurally differentiate the genome of *Secale cereale* L. from those of *S. montanum* Guss. and *S. vavilovii* Grossh. *Genetica* 43: 387-393.
- VETTEL, F. and W. PLARRE. 1955. (Several years experiments with heterosis in winter rye). *Zeitschr. f. Pflanzenzüchtung* 34: 233-238. (P.B.A. 26: 366).
- WENKERT, E., E. LOSER, S. N. MAHAPATRA, F. SCHENKER and E. M. WILSON. 1964. Wheat-bran phenols. *J. Org. Chem.* 29: 435-439.
- WHALEY, W. G. 1950. The growth of inbred and hybrid maize. *Growth* 14: 128-155.
- \_\_\_\_\_. 1952. Physiology of gene action in hybrids. In "Heterosis", Ed. by John W. Gowen. Iowa State College Press, Ames, Iowa.
- WIERINGA, G. W. 1967. On the occurrence of growth inhibiting substances in rye. Institute for storage and processing of Agricultural produce. Wageningen, Netherlands.
- WOLSKI, T. 1968. Niektóre ważniejsze problemy metodyczne hodowli żyta i ich podstawy genetyczne. (Some of the more important problems concerning methods of rye breeding and their genetic base). *Postepy Nauk Rdn.* 15(20): 89-106. (P.B.A. 40: 667).
- WRICKE, G. 1969. Studies on the inheritance of self-fertility in rye. *Theor. Appl. Genet.* 39: 371-378.
- \_\_\_\_\_. 1973. Inzuchtdepression und Genwirkung beim Roggen. (Inbreeding depression and gene action in rye). *Ibid.* 43: 83-87.



- ZEVEN, A. C. 1972. Plant density effect on expression of heterosis for yield and its components in wheat and  $F_1$  versus  $F_3$  yields. *Euphytica* 21: 468-488.
- ZILLMAN, P., B. E. McDONALD and E. N. LARTER. 1974. Palatability of triticale and rye when fed in diets for mice. (In press).

A P P E N D I X

APPENDIX I. ANALYSIS OF VARIANCE TABLES FOR THE ELEVEN CHARACTERS  
ANALYSED IN THE FIRST EXPERIMENT.

WEIGHT OF SEED SOWN.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
LINES	28	5.1874	0.1853	46.325**
AMONG INBREDS	10	0.8528	0.0853	21.325**
AMONG HYBRIDS	12	1.2663	0.1055	26.375**
HYBRIDS vs. INBREDS	1	0.3768		94.200**
HYBRIDS vs. GAZELLE	1	0.5414		135.350**
ERROR	87	0.3518	0.0040	
TOTAL	115	5.5392		

EMERGENCE.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	3560.9438	1186.9813	14.1181**
LINES	28	10088.7500	360.3125	4.2837**
AMONG INBREDS	10	3253.9094	325.3909	3.8685**
AMONG HYBRIDS	12	1633.2694	136.1058	1.6181
HYBRIDS vs. INBREDS	1	1701.4781		20.2286**
HYBRIDS vs. GAZELLE	1	12.6594		
ERROR	84	7065.4500	84.1125	
TOTAL	115	20715.1438		

DAYS TO HEADING.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	11.691	3.897	4.6895**
LINES	28	457.352	16.334	19.6558**
AMONG INBREDS	10	90.0073	9.007	10.8312**
AMONG HYBRIDS	12	84.8308	7.0692	8.5069**
HYBRIDS vs. INBREDS	1	105.4553		126.9017**
HYBRIDS vs. GAZELLE	1	0.8178		
ERROR	84	69.804	0.831	
TOTAL	115	538.847		

TILLERS PER PLANT.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	2.646	0.882	3.172**
LINES	28	61.292	2.189	7.8741**
AMONG INBREDS	10	6.9067	0.6907	2.4845*
AMONG HYBRIDS	12	10.3371	0.8614	3.0986**
HYBRIDS vs. INBREDS	1	37.3572		134.3784**
HYBRIDS vs. GAZELLE	1	0.8351		3.0040
ERROR	84	23.352	0.278	
TOTAL	115	87.290		

## APPENDIX I. CONTINUED.

HEIGHT.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	526.164	175.388	2.3591
LINES	28	15557.024	555.608	7.4735**
AMONG INBREDS	10	5223.7891	522.3789	7.0296**
AMONG HYBRIDS	12	1538.7323	128.2277	1.1248
HYBRIDS vs. INBREDS	1	4387.8369		59.0207**
HYBRIDS vs. GAZELLE	1	709.7163		9.5464**
ERROR	84	6244.896	74.344	
TOTAL	115	22328.084		

FLORETS PER HEAD.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	44.217	14.739	3.0777
LINES	28	4559.296	162.832	34.0013**
AMONG INBREDS	10	1304.3633	130.4363	27.2366**
AMONG HYBRIDS	12	151.6500	12.6375	2.6389**
HYBRIDS vs. INBREDS	1	1419.7081		296.4519**
HYBRIDS vs. GAZELLE	1	6.1883		1.2922
ERROR	84	402.276	4.789	
TOTAL	115	5005.789		

FERTILITY.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	143.289	47.763	1.9361
LINES	28	2040.412	728.729	29.5391**
AMONG INBREDS	10	3821.8679	382.1868	15.4920**
AMONG HYBRIDS	12	1083.5949	90.2996	3.6603**
HYBRIDS vs. INBREDS	1	11711.3322		474.7196**
HYBRIDS vs. GAZELLE	1	91.8860		3.7206
ERROR	84	2072.280	24.670	
TOTAL	115	4255.981		

SELF-FERTILITY (RYES ONLY).

SOURCE	D.F.	S.S.	M.S.	F-VALUE
LINES	25	66814.4945	2672.5798	14.7124**
AMONG INBREDS	10	15752.3800	1575.2380	8.6176**
AMONG HYBRIDS	12	6427.4736	535.6228	2.9846**
HYBRIDS vs. INBREDS	1	28097.9042		154.5073**
ERROR	78	14169.0841	181.6549	
TOTAL	103	80983.5786		

## APPENDIX I. CONTINUED.

YIELD.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	6399.189	2133.063	8.5811**
LINES	28	261685.144	9345.898	37.5974**
AMONG INBREDS	10	6720.7163	762.0716	3.0657**
AMONG HYBRIDS	12	16393.8415	1366.1536	5.4959**
HYBRIDS vs. INBREDS	1	225554.7052		907.3800**
HYBRIDS vs. GAZELLE	1	367.1552		1.4770
ERROR	84	20880.552	248.578	
TOTAL	115	288964.885		

YIELD AS % OF NORQUAY.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	22754.403	7584.801	16.5156**
LINES	28	309056.244	11037.723	15.3027**
AMONG INBREDS	10	5058.2818	505.8282	
AMONG HYBRIDS	12	50196.1123	4183.0094	5.7993**
HYBRIDS vs. INBREDS	1	235127.5201		325.9815**
HYBRIDS vs. GAZELLE	1	3.8150		
ERROR	84	60588.444	721.291	
TOTAL	115	392399.091		

HUNDRED KERNEL WEIGHT.

SOURCE	D.F.	S.S.	M.S.	F-VALUE
BLOCKS	3	1.029	0.343	4.0833**
LINES	28	116.284	4.153	49.4405**
AMONG INBREDS	10	16.4931	1.6943	19.6345**
AMONG HYBRIDS	12	6.0392	0.5033	5.9913**
HYBRIDS vs. INBREDS	1	55.3842		659.3357**
HYBRIDS vs. GAZELLE	1	1.2333		14.6821**
ERROR	84	7.056	0.084	
TOTAL	115	124.369		

APPENDIX II. CORRELATION COEFFICIENTS BETWEEN CHARACTERS AMONG THE ELEVEN INBRED LINES.

	ORIGINAL SEED WEIGHT.	EMERGENCE.	DAYS TO HEADING.	FERTILE TILLERS /PLANT.	HEIGHT.	FLORETS /HEAD.	OPEN POLLINATED FERTILITY.	SELF POLLINATED FERTILITY.	YIELD AS % OF NORQUAY.
EMERGENCE.	0.244								
DAYS TO HEADING.	0.353	-0.315							
FERTILE TILLERS /PLANT.	0.407	-0.162	0.359						
HEIGHT.	0.489	0.110	0.288	0.170					
FLORETS /HEAD.	0.527	-0.019	0.508	0.350	0.620*				
OPEN POLLINATED FERTILITY.	0.348	0.184	0.075	0.329	0.518	0.273			
SELF POLLINATED FERTILITY.							0.756**		
YIELD.	0.483	0.265	0.297	0.529	0.583*	0.486	0.719**		
YIELD AS % OF NORQUAY.	0.426	0.259	0.269	0.423	0.519	0.435	0.650*		0.888**
HUNDRED KERNEL WEIGHT.	0.589*	-0.093	0.578*	0.386	0.493	0.433	0.494		0.645* 0.609*

\* SIGNIFICANTLY CORRELATED WITH .05 PROBABILITY

\*\* SIGNIFICANTLY CORRELATED WITH .01 PROBABILITY.

APPENDIX II. CONTINUED. CORRELATION COEFFICIENTS BETWEEN CHARACTERS AMONG THE THIRTEEN HYBRID LINES.

	ORIGINAL SEED WEIGHT.	EMERGENCE. /PLANT.	DAYS TO HEADING.	FERTILE TILLERS /PLANT.	HEIGHT. /PLANT.	FLORETS /HEAD.	OPEN POLLINATED FERTILITY.	SELF POLLINATED FERTILITY.	YIELD AS % OF NORQUAY.
EMERGENCE.	-0.122								
DAYS TO HEADING.	0.099	-0.328							
FERTILE TILLERS /PLANT.	0.009	-0.207	-0.046						
HEIGHT.	0.333	0.103	0.116	-0.604					
FLORETS /HEAD.	0.014	0.024	0.184	0.091	0.070				
OPEN POLLINATED FERTILITY.	-0.423	0.052	-0.253	-0.087	0.170	-0.100			
SELF POLLINATED FERTILITY.							0.387		
YIELD.	-0.142	0.464	-0.150	0.468	0.378	0.258	0.231		
YIELD AS % OF NORQUAY.	-0.013	0.331	-0.109	0.143	0.212	0.126	0.145	0.475	
HUNDRED KERNEL WEIGHT.	0.391	0.048	0.432	0.124	0.337	0.357	-0.358	0.352	0.130

\* SIGNIFICANTLY CORRELATED WITH .05 PROBABILITY

\*\* SIGNIFICANTLY CORRELATED WITH .01 PROBABILITY.