THE CHARACTERIZATION OF THE F4 AND F5 GENERATIONS OF A SUBSTITUTIONAL TRITICALE UNDER NATURAL SELECTION, THE PATTERN OF RYE CHROMOSOME ELIMINATION AND ASSOCIATION OF RYE CHROMOSOMES WITH SOME AGRONOMIC CHARACTERS.

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Rosemary A. Giberson

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The characterization of F_4 and F_5 generations of a substitutional triticale under natural selection.

by

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A thesis 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

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ABSTRACT

Giberson, Rosemary A. M.Sc., The University of Manitoba, February, 1985. The Characterization of the F4 and F5 Generations of a Substitutional Triticale under Natural Selection, the Pattern of Rye Chromosome Elimination, and Association of Rye Chromosomes with some Agronomic Characters. Major Professor: Edward N. Larter.

The frequency of rye chromosomes in a population of F4 lines from a cross of a secondary triticale, 6A250 (x-Triticosecale Wittmack) x hexaploid wheat Anza (Triticum aestivum L.), was found to have decreased from the preceeding generation. Almost 60% of the F4 lines examined showed no detectable rye chromosomes. Chromosome 2R was the most frequently eliminated rye chromosome, followed by 4R, 3R, 6R, 7R, 5R and 1R, in descending order of frequency. From analysis of the F4 and F5 progeny, chromosomes 5R and probably 7R were associated with high percent total protein. Total protein levels were depressed by chromosomes 2R and 3R, but these chromosomes also carried loci which promoted high percent lysine levels. High kernel weight, high fertility and wheat type kernels were generally associated with three or fewer rye chromosomes. Kernel shrivelling did not appear to have an identifiable association with any particular rye chromo-

some in this population. Several of the lines examined were identified as being superior both in protein and agronomic attributes and were suggested as sources of improved breeding material for both wheat and triticale.

Chapter I

INTRODUCTION

The potential of rye genomic material (Secale cereale L.), for use in improving wheat (Triticum aestivum L.), is very high. For example, the substitution of rye chromosome 1R for 1B in some European and Mexican wheats was found to confer rust and mildew resistance in wheat. Attempts to simultaneously increase yield and protein have not generally been successful. Surveys of wheat related species have indicated (Johnson et al., 1979) that a relatively small pool of genomic material is available for use in transferring genes for high protein into commercial varieties. In the Secale family however, species generally contain higher protein than wheat (Villegas, 1970), and the hybrid species triticale (Triticosecale Wittmack), falls somewhere between. There exists considerable potential in transferring rye genomic material to wheat through the intermediary triticale.

Workers in triticale have observed that a great many of the genomic combinations of triticales are not agronomically favorable. Substitutional triticales (those bred back to wheat, resulting usually, in an incomplete complement of rye chromosomes) produced many superior triticale types. Some triticales were found to revert to the wheat morphology with

the concommitant loss of rye chromosomes, yet some retained good quality characteristics. It was also observed (Merker, 1975, Gustafson et al, 1984) that relatively few of the many possible genomic combinations theoretically possible from a mixed wheat-rye genome were found in breeder selected materials.

The present study was undertaken to determine the distribution pattern of rye(R) chromosomes in advancing generations of an unselected population of a secondary triticale originating from a cross between a primary hexaploid triticale (6A250; 2n=6x=42) and the common wheat cultivar, Anza (2n=6x=42). In addition, studies were made in an attempt to identify those rye/wheat genome combinations that resulted in agronomically superior lines that could be used as gene donors to commercial varieties, or as superior triticale parents.

Chapter II

LITERATURE REVIEW

Hybrids between species within the genera Triticum and Secale were first reported by Wilson (1876), Rimpau (1891) and Carman (1884). The hybrids were viewed only as curiosities until 1918. In that year Lebedoff accidentally produced a large number of hybrids by planting inter-rows of rye within a population of early winter wheat (Meister, 1921). The increasing attention paid to the hybrids resulted in the name "Triticale" being suggested by Lindschau and Oehler in a paper published in association with Tschermak (1936,1937).

The success with which triticales could be produced was markedly improved with the discovery of colchicine by Blakeslee and Avery, (1937) and Nebel and Ruttle (1938). Colchicine enabled workers to double the chromosome composition of the hybrid, thus stabilizing its genetic and cytological behavior.

Still, the relatively low level of fertility (seed set) of the triticale hybrids seriously limited its potential as a crop plant. With the great increase in numbers of hybrids however, it was discovered that triticales produced from different sources could be quite distinct from one another (O'Mara, 1948, Nakajima, 1950, Muntzing, 1935b, 1955, Shu-

lyndin, 1972). A wide range of heterogeneity existed in morphology, physiochemistry and in fertility among newly synthesized amphiploids.

2.1 TYPES OF TRITICALES

Different types of triticales were synthesized depending upon their chromosomal make-up. These were classified as either octoploids, hexaploids, or tetraploids. The earliest types were octoploid triticales, i.e., 2n=8x=56, with 42 chromosomes from the hexaploid wheat parent (Triticum aestivum L.) and 14 from the diploid rye parent (Secale cereale L.). Octoploid triticale, displayed good frost resistance and ability to grow on light soils, characteristics conferred by the rye parent. Winter octoploid triticales combined winter hardiness with earliness. Of particular interest was protein content, which could be higher than either parent. For example, Pissarev (1966) found that the growth rate of octoploid triticale (under local conditions in the USSR) to be better than that of wheat. When averaged over a period of 10 years, the protein content of triticale was superior at 18.41% versus a value of 13.51% for wheat (var. Moskovska). Breeders however, had to deal with the negative aspects of the octoploid type which contributed largely to a decreased yield. These factors included partial sterility, meiotic irregularities, poor straw strength and shrivelled kernels.

Primary hexaploid triticales (2n=6x=42) are the result of a cross of a tetraploid wheat (Triticum turgidum L., 2n=28) parent with a diploid rye (2n=14). The tetraploid wheat parent contributes the seven chromosomes from each of the A and B genomes to the hexaploid triticale while the rye contributes seven chromosomes from the rye genome. The first hexaploid triticales were produced from a cross of T. dicoccoides x S. cereale by Jesenko in 1913. Another by Schegalow (1924, from Muntzing, 1979) involved a cross of T. durum with rye. The first amphiploids, i.e. semi-fertile hybrids, were made by Derzhavin (1938) from a cross, T. durum x S. montanum. Some others included a cross by O'Mara (1948) of T. durum x rye, and T. turgidum x rye by Nakajima in 1950.

Through programs like those at Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) and the University of Manitoba, hexaploid triticales have undergone considerable improvement, viz. shorter, stronger straw, earlier maturity, better disease resistance, and improved yield. Although meiotic irregularities, aneuploidy and sterility have been reduced, these problems can still exist, depending upon the parentage involved.

The third class of triticales, the tetraploids (2n=28) have also been synthesized. Tetraploid triticales were produced by Krolow (1973, 1974, 1975), Chaudry (1968) and others. Krolow crossed hexaploid triticales(AABBRR) with di-

ploid rye to produce the three derivatives which genomically were: AARR, BBRR, and ABRR. These tetraploids were advanced through successive generations to the F6 or F7 at which point the level of aneuploidy was only about 2.5% making them more stable than most octoploid or hexaploid triticales. Because of their poor fertility, however, tetraploids have received little attention. More recently, tetraploid triticales analyzed by Gustafson and Krolow (1978) were found to lack either or both chromosomes 1B and 6B. These two B genome chromosomes are known to be contributors to meiotic instability in hexaploid wheat (Gustafson, 1983).

2.2 CROSSABILITY

The barriers to crossability between species of Triticum and Secale are known to be gene controlled. Two genes Kr1 and Kr2 located on 5B and 5A, respectively, in the dominant condition act as inhibitors of crossability (Lein, 1943; Riley and Chapman, 1967). The mode of action of the genes is to retard pollen tube growth at the style base and ovary wall. (Jalani, 1973; Jalani and Moss, 1977; 1980, 1981; Lange and Wojciechowska, 1976). Lange and Wojciechowska (1976) have shown that high crossability is associated with an increased number of functional pollen tubes being found at the micropylar end of the ovary.

The manifestation of the Kr1 and Kr2 genes appears to vary with levels of ploidy. Diploid wheats have a very low

crossability with rye (Sears, 1944; Katterman, 1941; Kiss, 1966; Krowlow, 1970, Moss, 1970). Tetraploid wheats crossed more readily, but the resulting seeds were shrivelled (Riley and Chapman, 1967; Moss, 1970). Jalani and Moss (1981) found three mechanisms controlling incompatibility. One, which seems to be typical for hexaploid wheats, is the above mentioned system of retardation of pollen tube growth. The second mechanism suppresses fertilization not withstanding the occurrence of a high proportion of "functional" pollen tubes being present near the micropyle. This mechanism is found in diploid wheats. The third mechanism which accounts for shrivelled seed development in tetraploids wheats, acts to cause endosperm failure after the onset of post fertilization development.

The grafting of wheat embryos onto rye endosperm has been reported to improve crossability between the two species (Pissarev and Vinogradova, 1944). Other workers have reported some positive results with the technique (Hall, 1954, 1956; Rommel, 1960; Moss, 1965) while other reports were less favorable (Tozu, 1966; Sanchez-Monge, 1956; Krolow, 1964). It appears that embryo transplantation does not result in an increase in the number of pollen tubes at the style base (Jalani and Moss, (1977), although there is evidence for a small increase in seed set (Hall, 1954, 1956; Rommel, 1960; Moss, 1965). Jalani and Moss (1981) suggested that embryo transplantation may act in improving the chances of fertilization and developmental success.

2.3 IDENTIFICATION OF CHROMOSOMES IN TRITICALE

The identification of rye chromosomes in triticale has been facilitated by the C banding technique (Singh and Lelley, 1975; Gustafson et al., 1976; Iordansk et al., 1978; Merker, 1973; Singh and Robbelen, 1975; Sarma and Natarajan, 1973; Gill and Kimber, 1974; deVries and Sybenga, 1976; Bennett et al., 1977; Sybenga, 1983). More recently, improvements in technique have made it possible to identify wheat chromosomes in addition to the rye chromosome complement (Gustafson et al., 1984; Gill and Kimber, 1974a,b). C banding has been useful in enabling workers to identify rye chromsome translocations (Kranz, 1976), substitutions (Lukazewski and Gustafson, 1983) and in establishing karyotypes (Sybenga, 1973).

The C banding technique involves the staining of specific masses of chromosomal proteins remaining after a denaturing treatment (Comings et al., 1973; Kongsuwan and Smith, 1978). The molecular action is believed to be the result of side-stacking of thiazin dyes to DNA (Comings, 1978; Sumner and Evans, 1973; Arrighi and Hsu, 1971). The DNA areas to which the dyes bind have been found via in-situ hybridization to consist of highly condensed, repetitive sequences although unique sequences are believed to be interspersed (Comings et al., 1973; Yunis and Yasmineh, 1970; Kuo and Hsu, 1977; Pardue and Gall, 1970). There is evidence that these areas are maintained, controlled and protected by tightly bound non-

histone proteins (Burkholder and Weaver, 1977; Comings, 1978, 1977; Paul, 1972). C bands specify areas of chromatin known as constitutive heterochromatin which it had been supposed, was inactive (Comings and Okada, 1975). Heterochromatin is characterized by remaining condensed throughout nuclear interphase and by beginning replication after euchromatic sections have already replicated (Comings, 1978; Yunis and Yasmineh, 1971; Paul, 1972).

Using C banding, Darvey and Gustafson (1975), Merker (1975), Vosa (1974) and others found that rye chromosomes exhibited dark staining, heterochromatic segments on their telomeres. The chromosomes of wheat did not exhibit these same telomeric blocks (Gill and Kimber, 1974b). Both wheat and rye exhibit small intercalary bands also, both show staining at the region of the centromere (Gill and Kimber, 1974b).

2.4 C-BANDING POLYMORPHISM

As well as typical C banding seen in many karyotypes (Sybenga, 1983), polymorphism of band patterns has also been reported (Weimark 1975; Lelley et al., 1978; Giraldez et al., 1979, Iordansky et al., 1978a,b; Singh and Robbelen, 1975; Bennett et al., 1977). Polymorphism has been attributed to unequal crossing over in the heterochromatic segments between homologous or even non-homologous chromosomes (Weimark, 1975; Bennett et al., 1977).

Differences have also been reported between open pollinated ryes which in general have more heterochromatin than inbred ryes (Giraldez et al., 1979). Wild species tend to have less DNA per chromosome and smaller terminal C-bands than cultivated ryes (Bennett et al., 1977). Gustafson et al., (1983) observed that rye chromosomes with deleted or amplified telomeric C-bands occurred spontaneously.

2.5 FERTILITY AND MEIOTIC STABILITY IN TRITICALE

Two major problems have been associated with the development of triticale, viz. aneuploidy and grain shrivelling. Progress has been made in improving the meiotic stability of hexaploid triticales (Gustafson and Qualset, 1975). Sanchez-Monge (1958) found his material to average 21 to 31.5% normal pollen mother cell production at first meiosis. Merker (1971) examined CIMMYT and U. of Manitoba triticales and found a range of 24 to 60% pollen mother cells to be normal. In the same study, Merker (1971), and Weimark in 1973, (in a study in octoploids) found that meiotic irregularities were correlated with the frequency of aneuploidy, but fertility level did not correlate with meiotic disturbance frequencies. Rupert et al., (1973) observed that fertility was correlated with meiotic disturbances in the early generations of a triticale, but became less associated with advancing generations. Others, (Riley and Chapman, 1957; Kempanna and Seetharam, 1972; Hsam and Larter, 1973; Merker, 1973) have also found that in advanced generations fertility and meiotic instability were unrelated.

Reasons for the disturbances in meiotic chromosome pairing are both genic and nucleotypic. Kaltsikes et al., (1980) proved that chromosomes which had failed to pair in metaphase I were asynaptic rather than desynaptic. The asynapsis theory is supported by Bennett et al., (1973) and Weimarck (1973, 1975b) who thought that the shorter period of chiasma formation in a triticale meiotic cell relative to rye, would tend to suppress pairing within the rye chromosome complement in triticale. Most univalents seen at metaphase I were in fact rye chromosomes (Pieritz, 1970; Thomas and Kaltsikes, 1976). Roupakias and Kaltsikes (1977a,b) however found no correlation between duration of meiosis and frequency of univalents.

Both wheat and rye have genic systems controlling chromosome pairing. The 5BL system in wheat acts to suppress homoeologous pairing (Okamoto, 1957; Riley, 1958). In the synthesis of a triticale, however, the 5BL system can be modified by the polygenic pairing system in the rye parent (Thomas and Kaltsikes, 1971; Lelley, 1976; Nakajima and Zennyosi, 1966; Miller and Riley, 1972; Riley et al., 1973; Naranjo et al., 1979; Dvorak, 1977).

Some of the most extensive cytological studies in triticale have focused on the heterochromatic telomeres of the rye genome (Bennett and Kaltsikes, 1973; Gustafson and Bennett, 1976; Thomas and Kaltsikes, 1974, 1976). Thomas and Kaltsikes (1976) observed that, of the predominately rye

univalents seen in metaphase I in triticale most had heterochromatic telomeres, and most rod bivalents were rye chromosomes paired at non-heterochromatic telomeres. The deletion of a heterochromatic block on the telomere of a rye chromosome was found to improve pairing (Roupakias and Kaltsikes, 1977; Merker, 1976; Naranjo and Lacadena, 1980).

Kaltsikes et al., (1983) synthesized triticales using a common wheat parent and various rye species containing different amounts of heterochromatin. No correlation between chromosome pairing and frequency of telomeric C-banding could be determined. However, it was pointed out that species differences within the rye parent and the fact that the heterochromatin on telomeres was only reduced, and not absent entirely, may act to mask any possible correlation between the two parameters.

2.6 KERNEL SHRIVELLING

Poor kernel development has been a serious problem in past triticale breeding programs. In the early triticales, the underdeveloped kernel was the result of the space enveloped by the pericarp being larger than the slow growing endosperm within, moreover internal cavities occurred within the endosperm itself (Thomas et al., 1980).

It has been observed that rye chromosomes tend to be associated with bridge formation in aberrant endosperm nuclei (Bennett et al., 1974, 1977; Kaltsikes et al, 1975). Heter-

ochromatin on the telomeres of rye chromosomes was thought to be responsible, but findings have been contradictory.

Darvey (1973) and Kaltsikes and Roupakias (1975) found in addition lines with chromosomes 2R, 3R and 7R, that fewer aberrant nuclei were observed in the endosperm when the telomeric heterochromatin on these chromosomes was absent. They further noted that the effect of adding a specific chromosome could be different from the effect of substituting that chromosome.

Gustafson and Bennett (1982) found a positive correlation between aberrant nuclei in endosperm and the presence of heterochromatin on the telomeres of chromosomes 4R and 6R. Improved test weight, thousand kernel weight and yield were associated with the deleted bands on chromosomes 4R. Chromosome 6R, although the deletion of the heterochromatic telomere was associated with a decreased frequency of endosperm aberrancy and an increased kernel weight, yield per se was not increased. A reduced fertility within the 6R substitution line apparently counteracted the increase in kernel weight. In a different gene background, Gustafson (1982) found the effect of chromosome 6R to be consistent with the previous findings.

However, Thomas et al. (1980) using telocentrics showed that for chromosomes 4R, 5R and 6R, kernel shrivelling was associated with the long arms of these chromosomes even

though the heterochromatic telomeric bands are carried by the short arms. It was further noted that in the triticale under study, the loss of heterochromatin from the long arm of 7R and short arm of 6R had no effect on kernel shrivelling.

More recently, Gustafson et al., (1984) examined eight triticale lines lacking chromosome 2R, together with a reduction of heterochromatin (6 to 8% vs 12%) and a chromosome 4R lacking the telomeric heterochromatin. No correlation was found between total heterochromatin content and frequency of aberrant endosperm nuclei.

2.7 SUBSTITUTIONS

Hexaploid wheat belongs to a unique group in nature. It is polyploid, containing three separate genomes derived, probably, from a common ancestor. The hexaploid wheats carry a "diploidizing" organizer on chromosome 5BL called the *Ph* locus which ensures that pairing between genomes does not occur. The A genome is derived from diploid wheat, probably *T. urartu Tum*, the D from *Ae. squarrosa L*, and the B genome resembles the S genomes of the Sitopsis section of the *Aegilops* genus (Miller, 1984). Sears (1966) demonstrated that extra chromosomes of one genome could compensate for the loss of particular chromosomes which were called homoeologues. There are seven homoeologous chromosome groups in bread wheat in which, for example, chromosome 1A can compen-

sate for its homoeologues 1B and 1D. The fact that these chromosomes can compensate for each other supports the concept of a common ancestor and indicates that no major structural rearrangements have occurred since divergence from that ancestor (Miller, 1984). Thus any member of the common ancestral Triticaea group such as the Secale sp. should, at least in theory, be capable of undergoing homoeologous chromosome substitutions with wheat.

A complete series of 21 monosomic deficiencies was developed by Sears (1954). A series of this nature facilitate the substitution of rye chromosomes for wheat. (For a description of the procedure, see Miller, 1984). When individual chromosomes of the rye genome are substituted for a wheat homoeologue, 1R, 2R, 3R, 5R, and 6R show close homoeology with their respective wheat counterparts (Miller, 1984). However, chromosomes 4R and 7R are believed to have undergone a translocation because each shows a partial homoeology with chromosomes in group 4 and 7 (Koller and Zeller, 1976).

Substitution lines can also be produced by crossing a hexaploid triticale of the genomic composition AABBRR to hexaploid wheat, AABBDD. Upon self fertilization, the resulting progeny, AABBDR, is capable of producing 128 genomic combinations ranging from a complete triticale (AABBRR) to a genomically pure wheat AABBDD (Gregory, 1974; Merker 1976). This method has been used to produce superior spring and winter triticales.

In addition to man made substitutions, naturally occurring spontaneous substitutions can also occur. For example, chromosome 1R was found to have replaced 1B in some European and Mexican wheat cultivars (Zeller, 1973; Mettin et al., 1978; Merker, 1975). These substitutions conferred rust and mildew resistance. Translocations have also been reported between rye and wheat chromosomes (see Driscoll, 1983 for catalogue).

2.7.1 Factors Influencing Rye Chromosome Elimination and Substitution

In the CIMMYT triticale breeding program, a superior selection obtained from an outcross of a triticale with a Mexican semi-dwarf bread wheat was found to have chromosome 2R substituted for chromosome 2D of wheat (Gustafson and Zillinsky, 1973). In a cytological examination of some of the CIMMYT lines, Merker (1975) found that substitutions of wheat chromosomes for rye chromosomes had occurred in some material. It was observed that the frequency of elimination of rye chromosomes was not random. For example, Merker (1975) found that 2R was the most frequently substituted chromosome while chromosomes 1R and 6R were least frequently substituted.

Out of 128 theoretically possible combinations in which seven rye chromosomes could be substituted for by wheat chromosomes, only a limited number have been identified (Gustafson, 1984). The pattern of substitutions observed

are likely the result of a combination of genic and nucleotypic interactions.

2.7.1.1 Genic Influences

Certain homoeologous chromosomes from the D and R genomes may have specific genes which make the substitution impossible. For example, chromosome 5R from S. montanum confers male sterility when added to Chinese spring (Miller, 1984). Attempts to substitute 4R of S. montanum for chromosomes of group 4 or 7 have been unsuccessful (Miller, 1984) even though substitutions with S. cereale have been made (Jenkins, 1966). Gustafson et al., (1984) noted that chromosome 2R which carries gene(s) for daylength sensitivity would have been much less favorably retained by the CIMMYT lines grown under short day conditions in Mexico than its substitution by 2D which carries gene(s) for daylength insensitivity.

Genotype specificities may govern the level of D/R substitution possible. For example, spring and winter type triticales differ in their retention of rye chromosomes. Lukaszewski and Apolinarski (1981) screened 83 winter triticales and seven F5 winter type triticale x bread wheat crosses. They found the bulk of the winter triticales (92%) retained a complete rye genome. Only one rye chromosome was lost in the winter triticales having an incomplete rye chromosome complement although five of the seven F5 derivatives had lost all rye chromosomes.

2.7.1.2 Nucleotypic Influences

Nucleotypic differences between wheat and rye also influence compatibility. Both the amount and type of DNA differ between wheat and rye. The smallest rye chromosome 1R is 24% larger than the largest wheat chromosome (5B). The largest R chromosome is 42% larger than 5B. (Gustafson and Bennett, 1976; Heneen and Casperson, 1973). Overall, the rye genome contains 33% more DNA (Bennett et al., 1977) than the largest genome in wheat.

As has been mentioned previously, not only does the R genome contain more DNA, but it contains proportionately more heterochromatic DNA than do the wheat genomes. The percentage of heterochromatic DNA varies between species, but in S. cereale with which most work has been done, about 12% of the DNA is heterochromatic (Miller, 1984). Most of the heterochromatic DNA in rye is in the form of telomeric heterochromatin. Heterochromatic DNA is late replicating, and this is also a well known cause of chromosomal disturbances during meiosis (Lima de Faria and Jaworska, 1972). Thus, nucleotypic factors might tend to cause the substitution of rye chromosomes which are least compatible with the wheat nucleus. This was observed in the case of 2R and 1R. (Gustafson and Zillinsky, 1973, 1978; Merker, 1975; Darvey and Gustafson, 1975). Chromosome 2R, the largest of the rye chromosomes, tended to be eliminated first, while 1R the smallest, was the last to be eliminated.

2.7.2 The Secale sp. as a Source of Desireable Agronomic Characters

The rye genome is an important potential source of desirable attributes for use in both triticale and as additions or substitutions into wheat. The substitution of 1R by 1B has been mentioned as a source of rust and mildew resistance in some European and Mexican bread wheats. Some of the desirable attributes of triticales also mentioned have been winter hardiness, ability to grow on light soils, early flowering and early maturity. Others are resistance to disease (Wabwato, 1974; Srivastava, 1974; Linde-Laursen, 1977; Stewart et al., 1968) and tolerance to acid and Al+ soils (Sapra et al., 1978, Sowa and Gustafson, 1980). One of the most important attributes that may be transferred from rye is the potential of improve the nutritional profile of wheat.

2.7.2.1 The Importance of Lysine Content

A nutritional diet for both humans and livestock must contain a balance of essential amino acids in the same proportion as used for growth and good health. If one amino acid in the diet is in limited supply, then the body can metabolize available resources only to the limit of the deficient amino acid. In wheat, the limiting amino acids are lysine and the sulfurated amino acids (Riley and Ewart, 1970; Kies and Fox, 1970).

Lysine levels in rye are superior to those in wheat, and triticale is intermediate to the two (Villegas et al., 1970;

Knipfel, 1969; Dexter and Dronzek, 1975). The discovery of mutants in maize which confer high lysine content in the grain (Mertz et al., 1964; Emerson et al., 1935) sparked a search for similar mutants in the other cereals. While no mutants have been found as of yet in wheat, it has generated interest in breeding for altered protein (Favret et al., 1969; Diehl et al., 1978; Lawrence et al., 1958; Schmidt-Stohn et al., 1980). The range available for increased lysine through breeding is quite small. Villegas et al., (1970) found a range of 2.15 to 2.77 g. per 16 g. N in spring wheat, from 2.32 to 3.42 in triticale, and from 2.55 to 4.26 in rye. Riley and Ewart (1970) added rye chromosomes individually to wheat and found that chromosome 5R increased lysine content by 8.7%.

Feeding studies have shown that large increases in lysine content are not required in order to make a substantial improvement in protein efficiency (Kies and Fox, 1970). For example, Mertz et al., 1964 fed lysine enriched corn to weanling rats and found a 3.5 fold increase in weight gain vs rats fed normal maize. Altschul (1971) reported increases of 60% in utilizable protein in wheat flour supplemented with 0.2% lysine.

2.7.2.2 Protein vs Lysine

In wheat and rye, total protein and lysine are thought to be negatively correlated, particularly if protein content is

low (Lawrence et al., 1958; Woodham et al., 1972; Villegas et al., 1970). In high protein lines, however this correlation diminishes. Johnson et al., (1978, 1979) examined a range of wheat lines for protein content and found that below 15% protein, an increase in lysine was associated with a depressed protein content. Above 15% however, high protein content had no effect on lysine level. A curvilinear relationship was reported in which 52% of the lysine per unit protein could be attributed to protein variation.

The negative association between protein and lysine is reflected in the ratios of the four fractions that comprise the endosperm protein. The water and salt soluble albumin and globulin fractions are significaantly higher in lysine than the glutenin and gliadin fractions. When the protein content of a line is increased, the glutenin and gliadins which are nearly devoid of lysine are increased at the expense of the albumin and globulin fractions. Thus in a high protein line there is proportionately less albumins and globulins and thus less lysine. If however, lysine is measured in another way, (expressing lysine as a percent of grain weight) lysine level increases with protein level (Johnson et al., 1979).

2.7.2.3 Genetic Controls of Protein Content in Wheat and Rye

Currently, it is believed that control of protein content in wheat is polygenic, each gene having a small additive effect

(Ausemus et al., 1967; Chapman and McNeal, 1970; Diehl et al., 1978; Kaul, 1964). It has been noted (Clark et al., 1928; Lebsock et al., 1964; Johnson et al., 1978; Halloran, 1975) that low protein appears to be at least partially dominant over high protein content. Otherwise, inheritance tends to values intermediate to the parents.

In rye also, partial dominance for low protein operates in a poly- genic system (Plarre and Fischer, 1975; McLeod, 1979). Thus high protein results from the accumulation of recessive alleles.

2.7.2.4 Chromosomal Control of Proteins

Genes controlling the synthesis of seed storage protein are found on chromosomes 1A, 1B, 1D of wheat and 1R of rye. (Morris, 1984 for review). Long arms of 1A 1B and 1D carry Glu-1 genes which control the production of high molecular weight glutenins (Payne et al., 1983). A second gene, Sec-3, controls the equivalent high molecular weight secalins on the long arm of 1R (Lawrence and Shepherd, 1981). The Gli-1 genes controlling gliadin production are found on the short arms of 1A, 1B and 1D (Payne et al., 1983), while the gene Sec-1 which controls the equivalent secalins is located on the short arm of 1R. Other secalins are controlled by genes also on 1R and on 2R. Shepherd and Jennings (1971) also noted the control of 1R over gliadin proteins in rye. In wheat, a further gliadin controlling set of genes, Gli-2

exist on 6A, 6B and 6D (Payne et al., 1983) but they appear to have no exact counterpart in rye.

Morris et al., (1973) in a monosomic analysis of wheat cv. Atlas 66, indicated that chromosome 5D and possibly 5A and 5B were involved in controlling high protein. Substituting 2R of rye for group 2 chromosomes in the wheat cultivar Chinese Spring resulted in higher grain protein content (Jagannth and Bhatia, 1972). Olmedo et al., (1977) found all chromosomes of hexaploid wheat to be involved in the genetic control of various fractions of endosperm protein. In rye, Riley and Ewart (1970) found 5R (I), when added to wheat increased levels of both cystine and lysine. Threonine content was reduced by the addition of chromosome 7R.

2.7.2.5 Environmental Influences on Protein Content

Environment, soil and the cultivar are major factors affecting grain protein levels (Schlehuber and Tucker, 1959; Diehl et al., 1978). Miezan et al., (1977) in an extensive study of the effects of environment and genetic influences on grain protein in 12 locations concluded that genetic factors influenced grain protein content to a similar extent as environment.

Campbell and Picket (1961) qualified this with the observation that (in sorghum) narrowly adapted, local varieties when grown over a range of environments did indicate that a major portion of variability was due to environment. How-

ever, cultivars having a wide range of protein in the genotype, gave indications that the major portion of variability was due to genotype.

Chapter III

MATERIALS AND METHODS

A total of 223 secondary triticales (X Triticosecale Wittmack) were used in the present study, all of which originated from a cross between a University of Manitoba primary triticale Accession 6A250, and Anza (Triticum aestivum L.) (Gustafson and Zillinsky, 1978). The genomic constitution of 6A250 was established as AABBRR (Sowa and Gustafson, 1980). 6A250 (AABBRR) crossed with Anza (AABBDD) resulted in a hybrid of AABBD(R) constitution, the progeny of which were self fertilized to the F5 generation. Because of its genomic composition, the AABBD(R) hybrid exhibits an irregular meiosis. The D and R genomes, due to the absence of regular pairing homologs, exhibit random distribution in the gametes. The progeny would theoretically, range from a pure triticale (AABBRR) to a pure wheat (AABBDD).

At the F4 generation, each of the 223 lines was analyzed for total protein content, lysine content, thousand kernel weight, and, kernel appearance. A random sample of 32 of these lines were C banded in order to determine their genomic constitution. The F5 generation was again analyzed for protein content, lysine content, and fertility. This generation of material was sown at two sites, one at the Univer-

sity of Manitoba, as was done for the F4, and an additional site at University of California at Davis.

3.1 KERNEL EVALUATION

The F4 generation lines were visually rated on a scale of 1 to 4; the lower range of the scale representing those samples that were wheat-like in hardness, color and translucency. The upper end of the scale represented those kernels classed as triticale-like.

The degree of kernel shrivelling was also considered on a visual basis of the F4 generation. Seeds were rated on a scale of 1 to 4; 1 being plump, 4 being shrivelled.

3.2 PROTEIN ASSESSMENTS

Total protein content was determined for each of the 223 lines at each site using micro-kjeldahl procedures. Findings were expressed as nitrogen (N) x 5.7 at 14 percent moisture.

Lysine content was determined using an automatic amino acid analyzer Beckman model 121. Content was expressed as a percent of total protein. As in the case of total protein, analyses were made for the F4 at University of Manitoba, F5 at University of Manitoba and F5 at the University of California at Davis.

3.3 FERTILITY ESTIMATES

Fertility estimates were made by determining the average number of seeds/spikelet from the four best spikes. Material from the F5 generation only was available for analysis.

3.4 CYTOLOGICAL STUDIES

In order to identify specific chromosomes involved in genomic constitutions, root-tip chromosomes were C banded according to the method of Darvey and Gustafson (1975), or a modification of this technique (see b., below). The modified technique was necessary to achieve better spreads and staining of some samples in which the standard method was unsatisfactory. Random samples were taken from the population of 223 secondary triticales, and a total of 32 of these were successfully C banded and analyzed for the presence of rye chromosomes.

For cytological purposes, root-tips were treated in (a): a solution of 0.005 g of 8-hydroxy- quinoline and 0.01 g of colchicine per 10 ml of distilled water for a period of 3.25 hrs. at 18-20^{o} C. Root-tips were then fixed and stained in a 1.5% solution of aceto- orcein followed by a further 3 hour treatment in fresh aceto-orcein diluted 9:1 in 2N HCl. A squash preparation of each root tip was made in a drop of 45% acetic acid. A cover slip was applied using a cytological press (Larter and Ikonen, 1977) for purposes of obtaining uniformity of chromosome spreading. Squash preparations

were freeze-dried with carbon dioxide after which the cover slips were removed. The squashes were then air-dried for 2 hours, after which they dehydrated in a sequence of 70% alcohol for 30-50 minutes, 95% for 1 hour, and 100% for 15 minutes. Slides were then air-dried for 24 hours. The preparations were then placed in a saturated solution of barium hydroxide for 5-6 minutes at 25° C; then rinsed in deionized water for 2-3 minutes. Slides were placed in a room temperature solution of 2XSSC whose temperature was heated to 52-56° C in a water bath for 2 hours. Slides were then removed, stained in Leishman's stain diluted 1:4 in phosphate buffer at pH6.8 for a variable length of time, depending on the age and manufacturer of the stain. Stained preparations were then briefly rinsed, air dried overnight, cleared in xylene and mounted in permount.

(b): The alternative method was to pretreat root-tips in a solution of 0.005 g of 8-hydroxyquinoline and 0.01 g colchicine per 20 ml of distilled water for approximately two hours at 28° C. They were then fixed in 45% acetic acid overnight, followed by staining in a solution of 9 parts 1N HCl to 1 part 1.5% aceto orcein overnight. The root-tips were then rinsed in distilled water, softened in 5% pectinase for 20-30 minutes. A squash preparation was made in a drop of 45% acetic acid, then freeze dried, the coverslip removed and the slide was dried for 2 hours. Preparations were then dehydrated through a sequence of 70% alcohol for

10 minutes, 95% for 1.5 hours and 100% for 10 minutes, followed by drying overnight. The squash preparations were then dipped in a saturated solution of barium hydroxide for 5 minutes, rinsed, and treated for 10 seconds in 0.1 N NaOH freshly made. Slides were transferred to a solution of 2XSSC at room temperature for 5 minutes twice. This was followed by a treatment in 0.3XSSC twice for 30 minutes, after which the slides, in 0.3XSSC, were transferred to a 56-58° C water bath for 1 hour. Slides were then immersed in dilute (20:1) Leishmans' stain with half strength phosphate buffer for 12-15 hours. Slides were then dried, cleared in xylene and mounted.

Chapter IV

RESULTS AND DISCUSSION

4.1 TOTAL PROTEIN

Values of percent total protein (at N x 5.7% and 14% moisture) for the 223 lines are charted in Figures 1-3 for the three sites under study - the F4 at the University of Manitoba, the F5 at the University of Manitoba and at the University of California at Davis. In 1978 the F4 protein content fell between the 12 and 16 percent classes (the wheat parent Anza and 6A250 respectively). In the F5, grown in 1979 at 2 sites (Davis, California and the University of Manitoba) protein distributions broadened and shifted upward on the scale. The Davis, California site showed a broader distribution and higher protein values than the University of Manitoba site of the same year/generation.

Analysis of variance between 1978 at the University of Manitoba and 1979 at the same location gave an F value of 61.51 at P=0.0001 indicating that differences between years and generations was highly significant. As has been realized by others (Clark, 1926; Diehl et al., 1978), protein and other agronomic characters can be greatly influenced by environment. Differences between the F4 and F5 genomic constitution might also exist due to the elimination of rye

chromosomes and their substitution by wheat chromosomes. Thus it is not possible to directly compare protein content of the three sites under study.

When the lines which ranked in the top 10% total protein from each site were compared, two categories could be identified. (Table 1). Approximately 50 percent of the lines which appeared in any one year with high protein, would again be found in the top 10% at another site. However, the remainder of the lines did not appear more than once.

Similarly, when the lowest 10 percent protein classes were compared by site, approximately one half of the lines appeared in the top 10% class in at least two sites. (Table 2). The remainder were not found more than once. Only one line (20378), ranked in the top 10% protein class for all three sites.

The common parent of all the lines is the wheat cultivar Anza. However, environmental effects coupled with the presence or absence of specific rye chromosomes and, the presence of D genome chromosomes which have substituted for missing rye chromosomes, all create a mileiu for multiple interactions. It has been found (Diehl et al., 1978) that crosses made to develop high protein wheats generally produce lines whose protein yields vary largely with environment and which may vary in rank relative to each other. A portion of the lines in this study repeated this pattern,

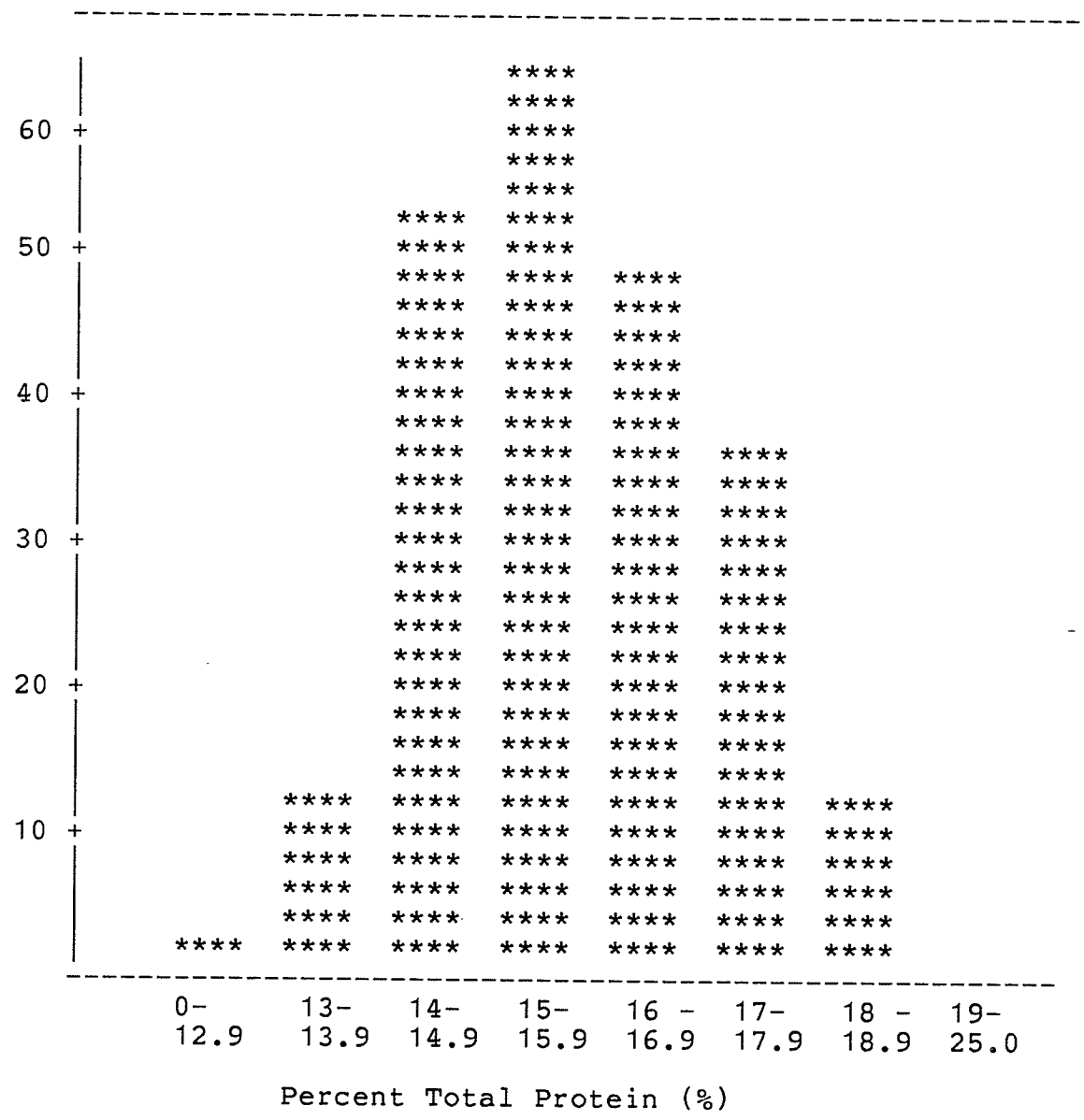

Figure 1. The distribution of percent total protein of F4 progeny from a cross of 6A250 x Anza grown at the University of Manitoba in 1978.

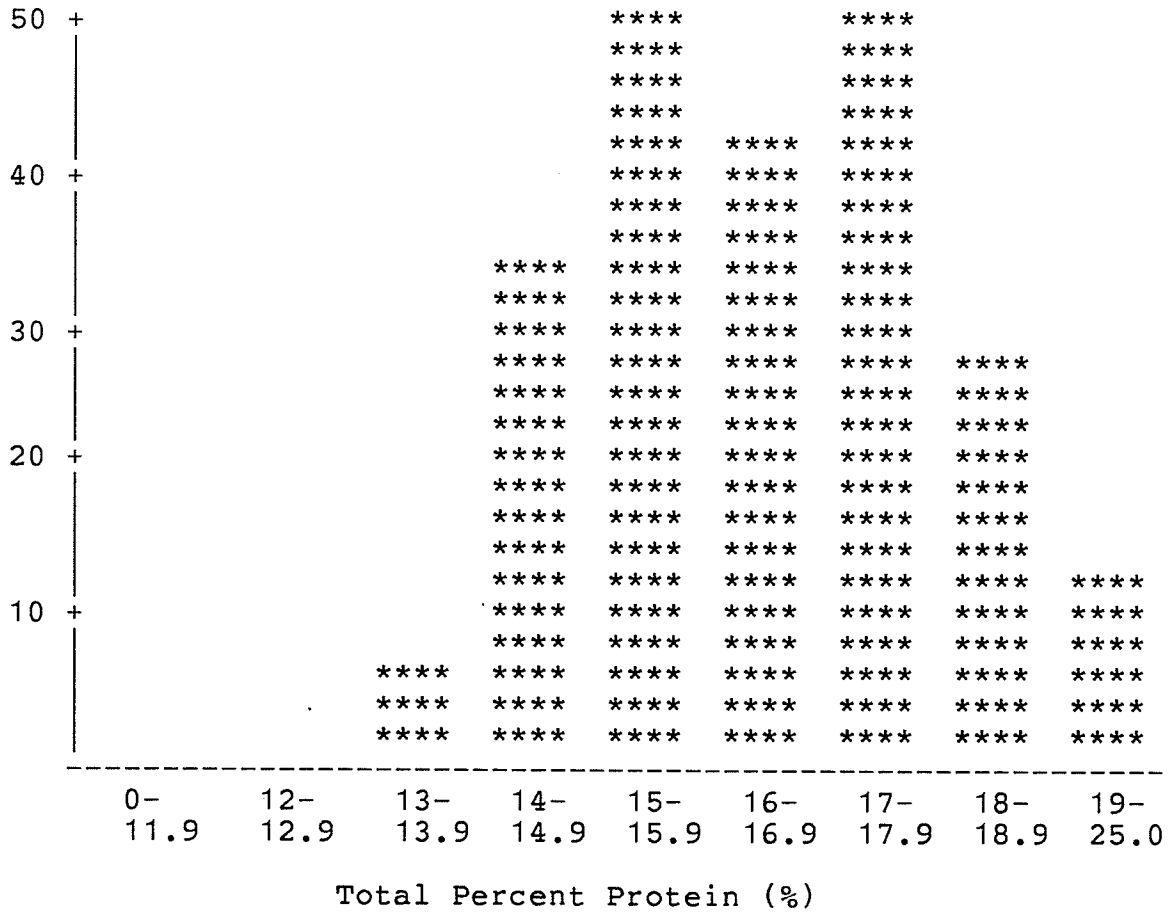

Figure 2. The distribution of percent total protein of F5 progeny from a cross of 6A250 x Anza grown at the University of Manitoba in 1979.

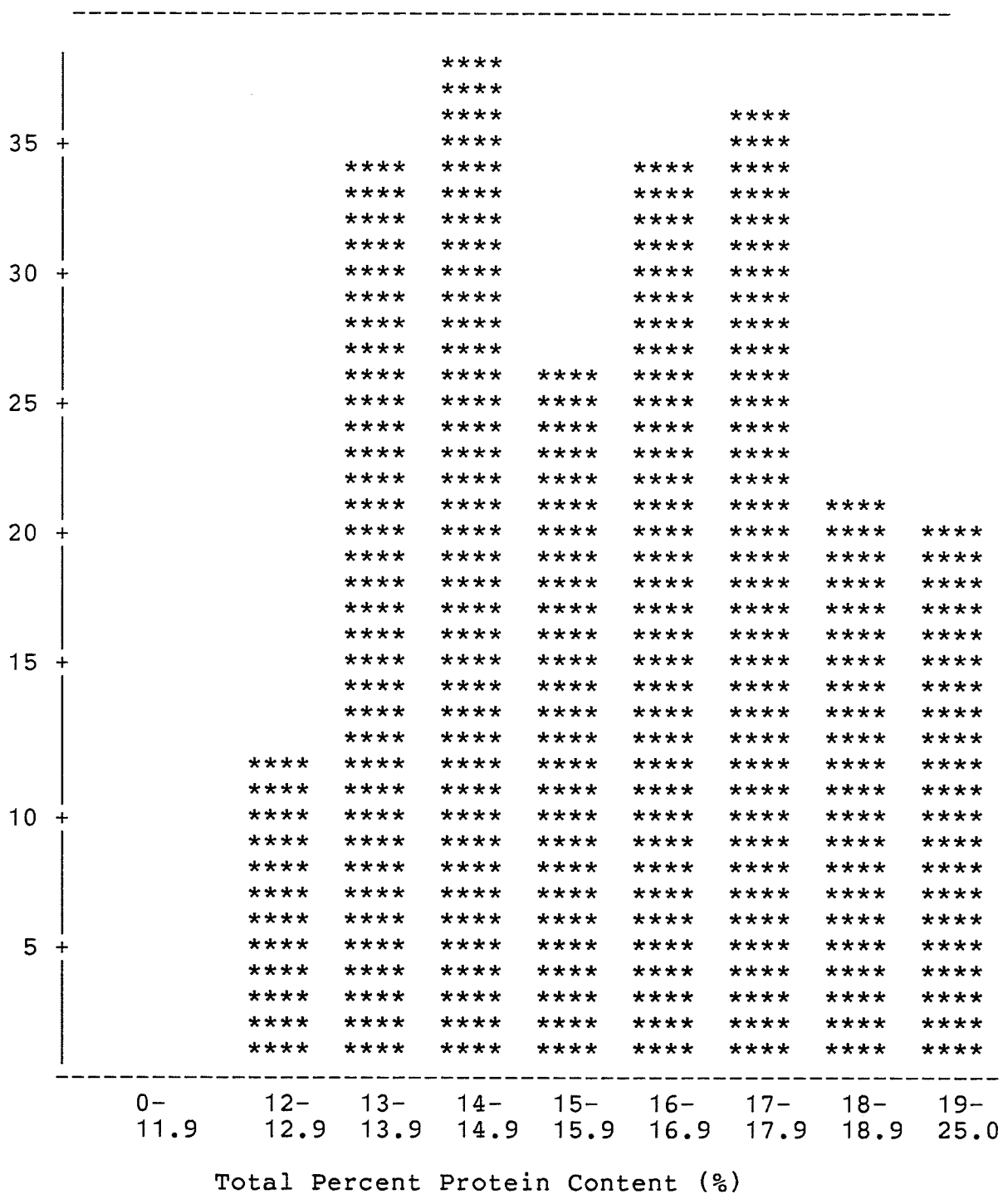

Figure 3. The distribution of percent total protein of F5 progeny from a cross of 6A250 x Anza grown at the University of California, at Davis, in 1979.

Table 1. Best 10% of progeny for percent total protein from a cross of 6A250 x Anza.

F4 Generation	F5 Generation	
1978	1979, U. of M.	1979, Davis.
20933	20562*	20246
20124	20564*	21063
21068*	20539*	21869
20053*	21338	20053*
20099*	20573*	20563*
20606*	20053*	21641
20601	20378*	20617
21021*	20606*	21166*
21842	21166*	21335
21549	21613	21221
20098	20497	20099*
20252*	21068	21043
20539*	20248*	20378*
20562*	21200*	20406*
21122	21288*	20588*
21288*	20407*	20564*
21593	20588*	20970
20283	21583	20407*
20378*	20252*	20408
20573*	20406*	21164*
21200*	21167	21021
20248*	20251	21028
	20563*	
	21164*	

Lines are listed in descending order of rank.
*Indicates that the line appears in another site.

but of interest are those which tended to retain their rank over time and location. Those lines which tended to remain in the high protein ranks may be more widely adapted types in which the environmental influence is reduced. Lines which changed rank are likely narrowly adapted types with a significant environmental influence.

Table 2. Lowest 10% of progeny for percent total protein from a cross of 6A250 x Anza.

F4 Generation	F5 Generation	
1978	1979, U. of M.	1979, Davis.
20893*	21793	21608
20419	20203	21791*
21365	21661	20221
20486	20864	21792
20330*	20059	21589
20362*	21230	20244
21731	21060	20404
20430	20862	21738
20298	20819	21721
20167	21522*	21081
21862	21079	20716*
21795	20362*	20362*
21791*	20045	20207
21785	20893*	21820
21869	20789	21636
21857*	20361	21522*
20805*	20330*	21480
20664	20279	21250
20299	20805*	20661
21855*	20704	21855*
21792*	20603	20156*
21428	20524	20017
20716*	21869	21080
20156*	21857*	20709

Lines are listed in ascending order of percent total protein.
*Indicates that the line occurs in another site.

4.2 LYSINE

Figures 4-6 illustrate the distribution of percent lysine content of the F4 and F5 generations.

Variability in lysine content was quite narrow relative to that seen for total protein, with 1978 readings ranging from 2.5 to 3.5%. In 1979 at both the Davis and University of Manitoba sites, values were again to be found in the 2.5 to 3.5 percent range, although variability had decreased due to the elimination of values in the classes on both extremes (c.v. of 10.9 in 1978 vs 8.7 at the University of Manitoba in 1979 and 8.1 at the University of California in 1979). The range found in the present study compares with that of Johnson et al., (1979) in which lysine values from a broad spectrum of wheat species ranged over a narrow band between 2.56% and 3.58%. Low levels of variation due to environmental influences has also been observed elsewhere (Miller, 1950). Lawrence et al. (1958) also in a study of Triticum and related species found that lysine content underwent little variation over the three years and three locations tested, except as affected by total protein level.

When the lines in the top 10 percent lysine class were ranked, approximately two-thirds of the population in this class were consistent in appearing in at least one other site (Table 3). Five lines appeared in all three sites. Although absolute values varied with site, a good number of lines exhibit a consistency which may indicate a reduced genotype x environment interaction.

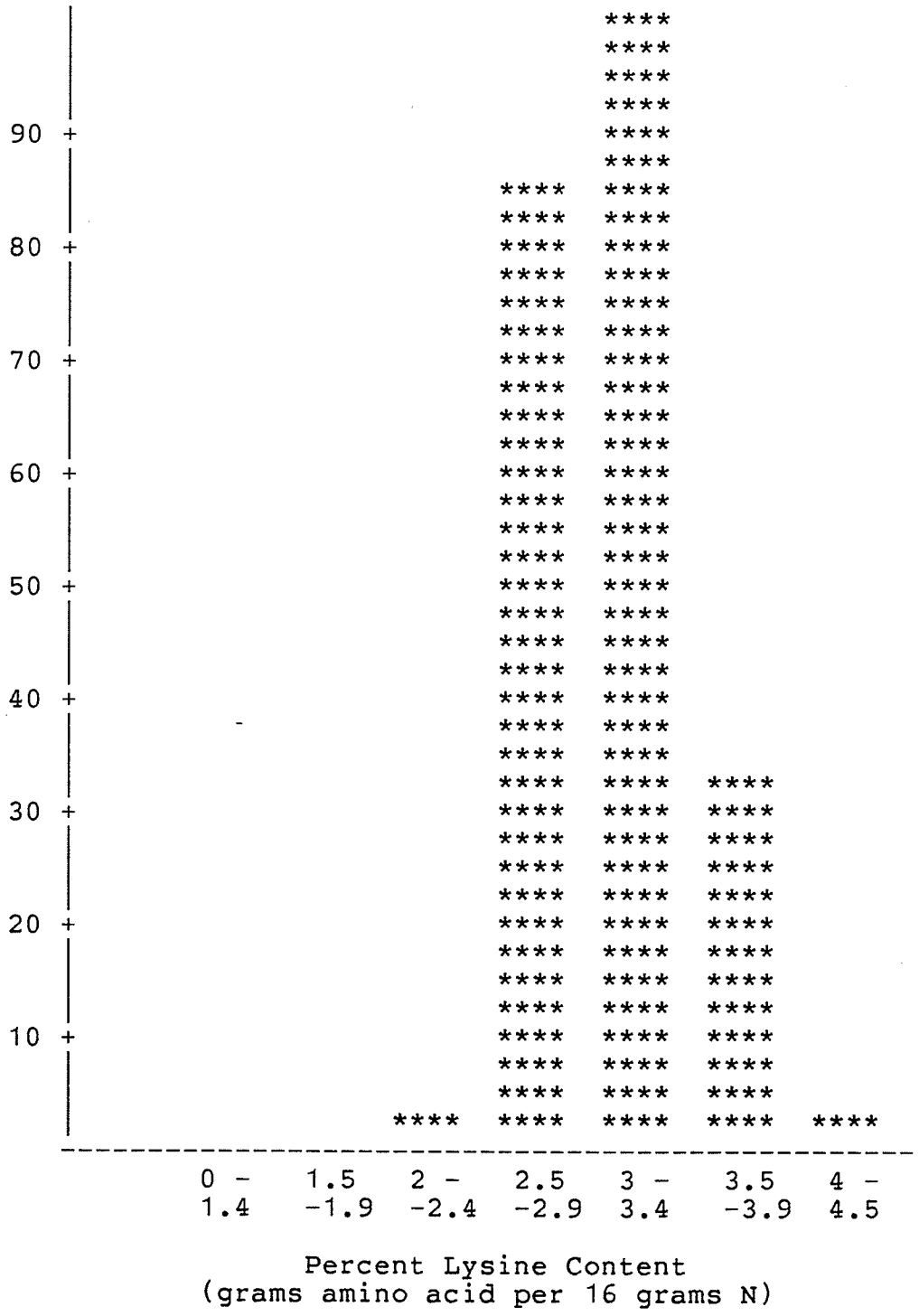

Figure 4. Lysine distributions of the F4 progeny from a cross of 6A250 x Anza grown at the University of Manitoba in 1978.

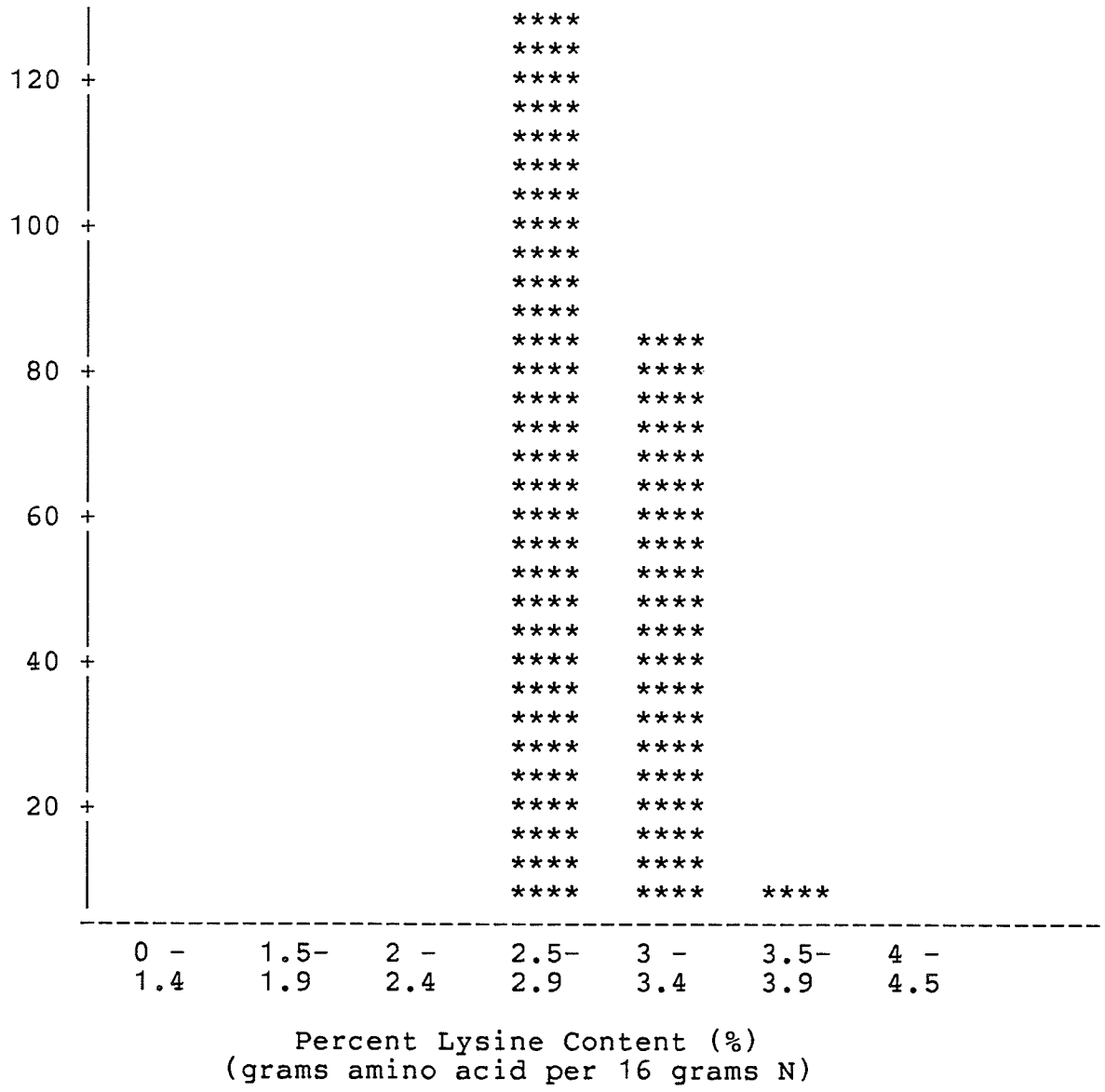

Figure 5. Lysine distributions of the F5 Progeny from a cross of 6A250 x Anza grown at the University of Manitoba in 1979.

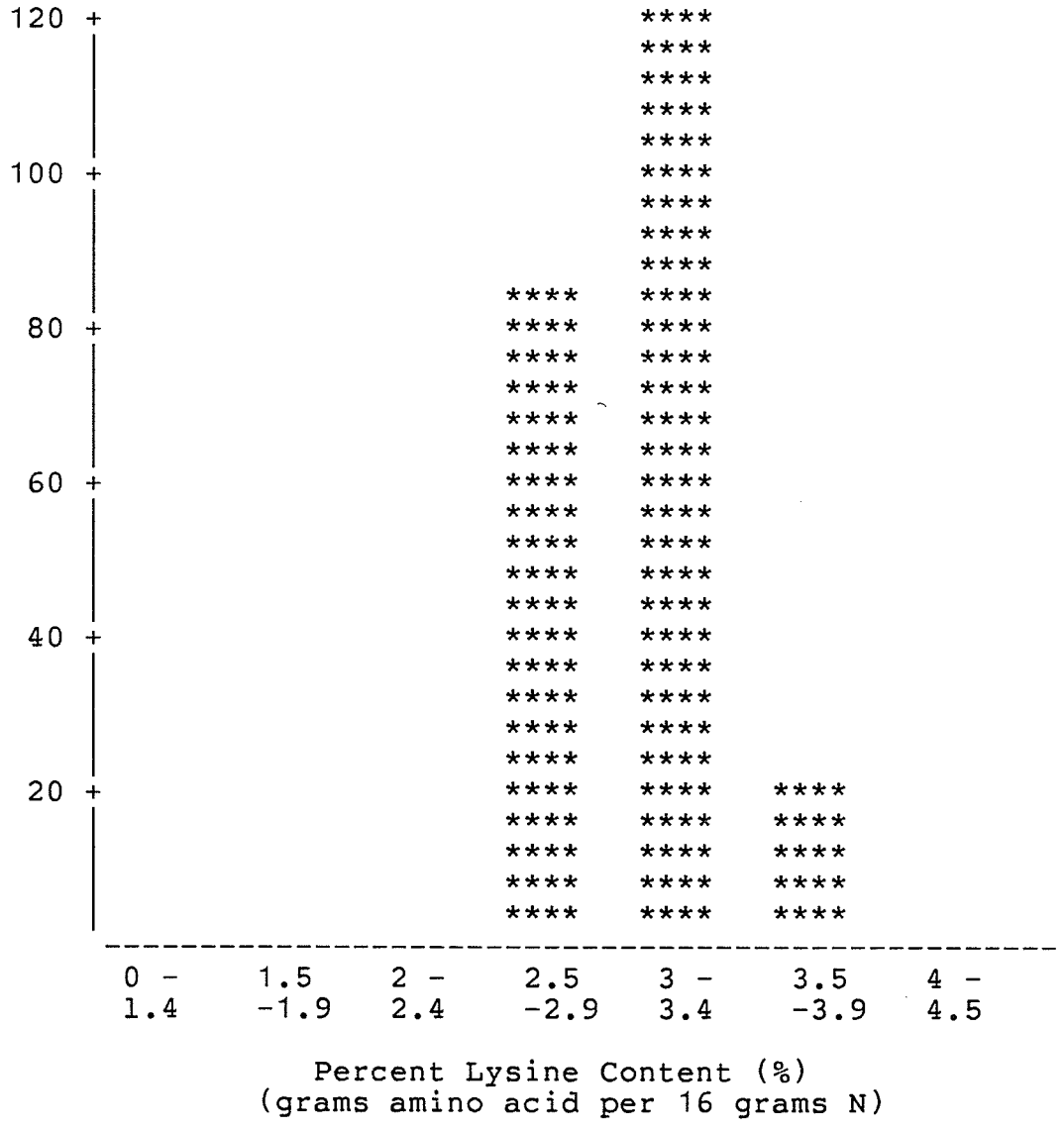

Figure 6. Lysine distributions of the F5 Progeny from a cross of 6A250 x Anza grown at the University of California, at Davis, in 1979.

Table 3. Best 10% of lines for percent lysine of progeny from a cross of 6A250 x Anza.

F4 Generation	F5 Generation	
1978	1979, U. of M.	1979, Davis
21365*	21063*	21791*
20424*	20524*	21164
20419*	21785	21855*
21588*	20946	21862*
21707	21588*	21773
20486	20804	21789
21862*	20419*	20430
21063*	20805*	20805*
20246	20203*	20156
21795*	20485	21857*
21167	21862*	21221
20937*	21857*	21589
20524*	21869	21792*
20407	20933	20424*
21791*	20424*	20526
21200	21792*	20617
21793*	20970	20099
20805*	21793*	20494
21388	21795*	20497
20633	21855*	20203*
21428	20937*	20937*
21682	21365*	21793*

Lines are listed in descending order of percent lysine.
*Indicates that the line appears again in another site.

The lowest 10 percent lysine class shows much less reproducibility between sites than the top 10% lysine class

(Table 4). Only seven lines appear more than once, and only one of these over all three sites. In this case, only a few lines show reduced independence from environment unlike the high lysine class. Variable effects of environment may be due to the polygenic system governing protein control. Under this multi-allelic system governing protein, it is possible that some systems may be more sensitive to environment than others.

Ranges between so called "high" lysine and "low" lysine types were not great - generally a difference of one or two percent. In view of Altschul's (1971) observation that a 0.2 percent supplement in lysine content can improve protein utilization by 60%, the differences exhibited in this population are significant.

Table 4. Lowest 10% of lines for percent lysine in the progeny from a cross of 6A250 x Anza.

F4 Generation	F5 Generation	
1978	1979, U. of M.	1979, Davis.
20052	20514*	20053*
21773	20648	20248
20497	20620	20486
20697*	20697*	21504
20196	20581	21731
20195	20248	20247*
21481	20485	20609
20819	21842	20251*
20514*	20710	21734
20251*	20709	20250
20175	21583	21842
20247*	20588	20563
20464	20539	20524
20053*	21593	20254
20252	21590	20952
20207*	20251*	20700
21641*	21641*	21320
20408	21179	21335
20154	21613	20710
21636	20716	20485
20711	20342	20299
21735	20207*	20244

Lines are ranked in ascending order of percent lysine.
*Indicates that the line has appeared in another site.

4.3 RELATIONSHIP OF PROTEIN AND LYSINE

Regressions were run between percent lysine and percent protein for the F4 and F5 generations. Scatter diagrams produced from data from the three sites illustrate the range of

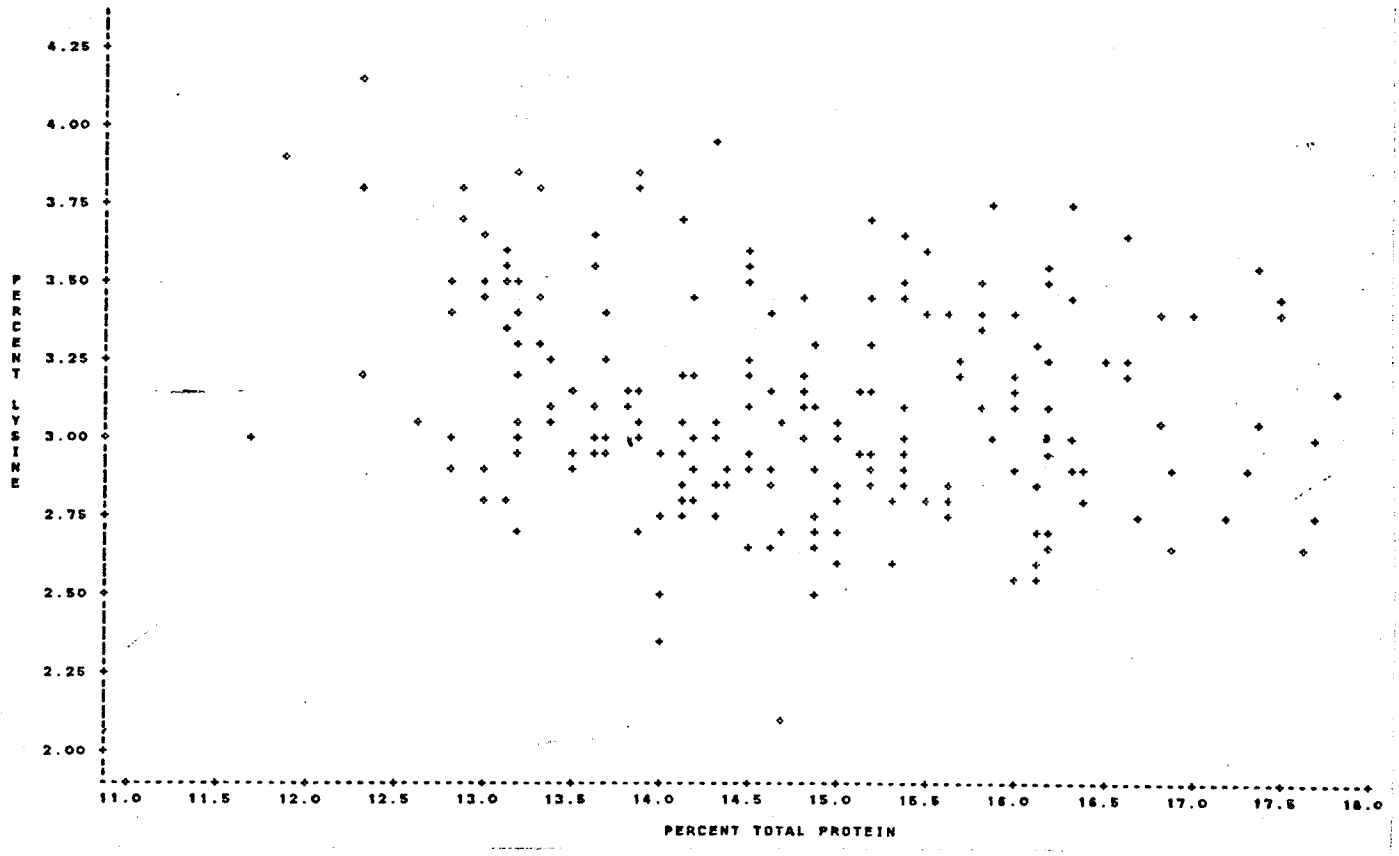

Figure 7. Plot of percent lysine vs percent total protein content of the F4 progeny from a cross of 6A250 x Anza grown at the University of Manitoba in 1978.

values for the lines tested (Figures 7 to 9). The scatter

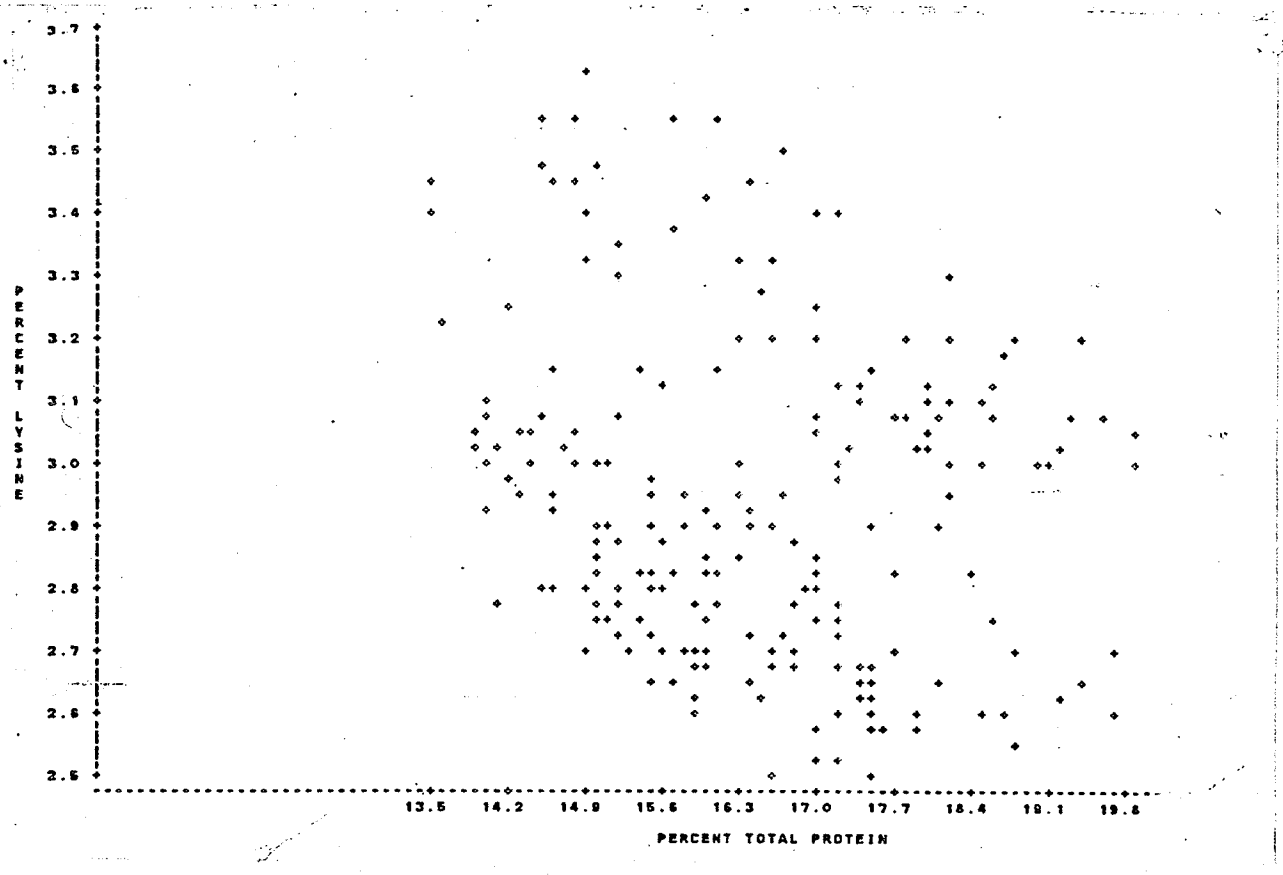

Figure 8. Plot of percent lysine vs percent total protein content of the F5 progeny from a cross of 6A250 x Anza grown at the University of Manitoba in 1979.

plots show that for any of the three sites the current population does not closely fit the accepted inverse relationship between protein content and lysine levels (Johnson et al., 1979; Villegas et al., 1970). There is observed a small but significant negative correlation at the University of Manitoba sites r=-0.19, (P=0.01) and r=-0.20 (P=0.01) in

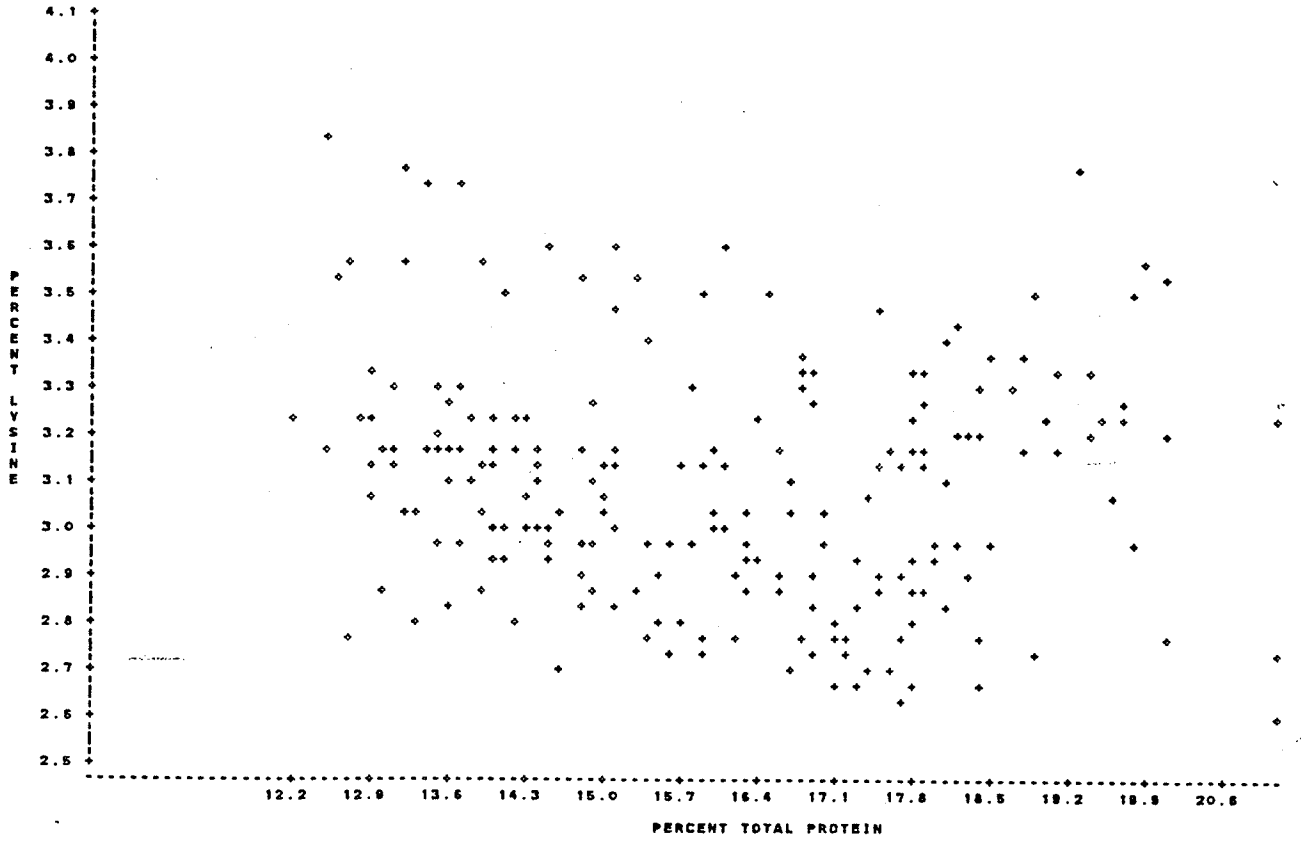

Figure 9. Plot of percent lysine vs percent total protein content of the F5 progeny from a cross of 6A250 x Anza grown at the University of California at Davis in 1979.

1978 and 1979 respectively. At the Davis site, r=-0.12 but was not significant (P=0.10). The relatively low although significant correlations observed in this study are substantially less than those found by Johnson et al., (1979) who determined that "52 percent of the variation in lysine per unit protein among common wheats in the World Collection is

attributable to variation in protein content." Villegas et al. (1970), found that a highly significant correlation between total protein and lysine in one location in a class of wheat, was not necessarily duplicable in another location. The variability between locations of the F5 generation fits the trend observed by Villegas.

Lawrence et al. (1958) found that if he used 13.5% as a breakpoint in the range of protein values that he found in wheat, values below this level were highly and inversely correlated with lysine levels (r=-0.73). For percent protein values above 13.5%, no correlation was found. This relationship was also observed by Villegas et al. (1970). It was expected that the variation in the present population would be greater than that found in Johnson's study because of its diverse genetic composition (wheat and triticale). The rye component may be responsible for the deviation from the curvilinear relationship between total protein and lysine as found by Johnson (1979) and Muntz et al., (1979) in wheat.

4.4 KERNEL WEIGHT

The distribution of values for kernel weight as determined from the F4 lines studied is illustrated in Figure 10. The largest class (25.0-27.5 g/1000 kernels) includes values for both the Anza and 6A250 parents. The population falls as a near normal distribution around a mean of 27.3 g, with val-

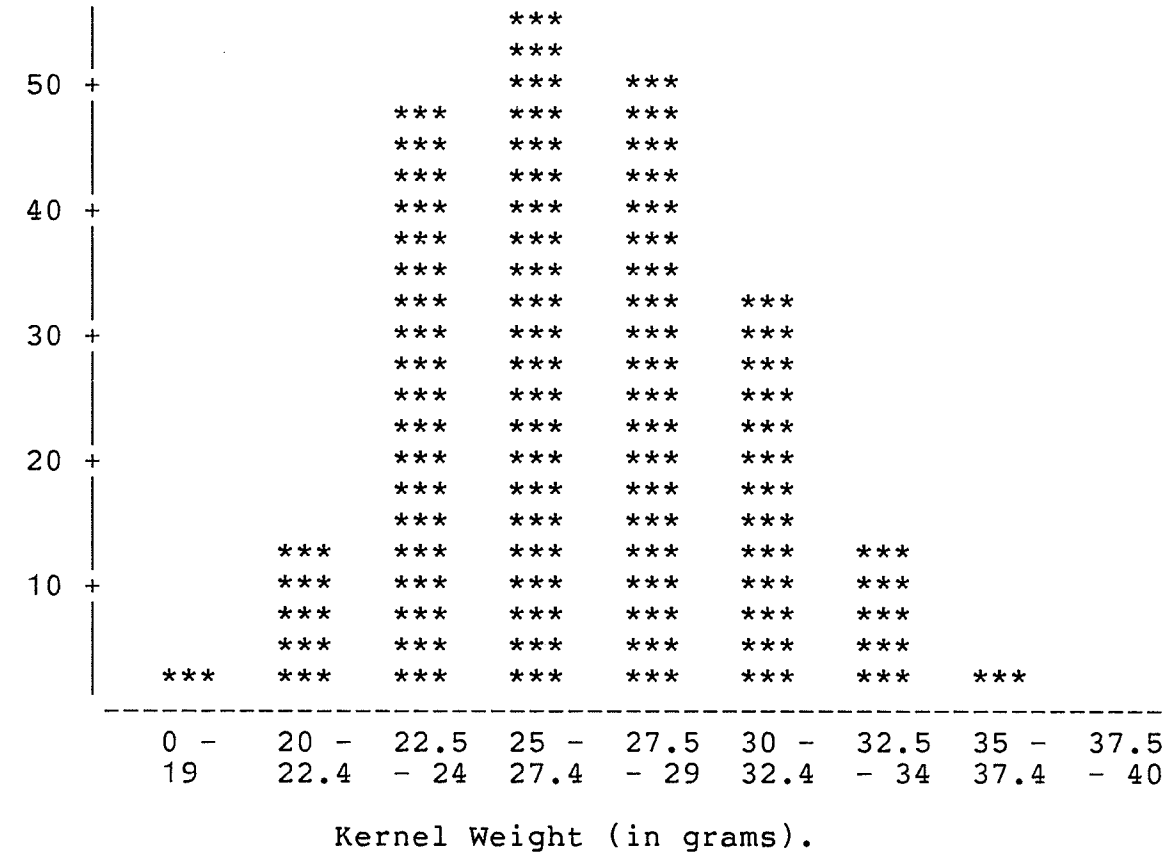

Figure 10. The distribution of kernel weight assessments of the F4 progeny of a cross of 6A250 x Anza grown at the University of Manitoba in 1978.

ues ranging from 16 to 39.7 g/1000 kernels. Kernel weight evaluations showed no significant correlations with any of the variables studied.

4.5 KERNEL TYPE

4.5.1 Kernel Appearance

The evaluation of kernel appearance made on a visual basis with the F4 lines is illustrated in Figure 11. Class 1 represents those kernels most wheat-like in color and appearance of the seed coat, while class 4 includes those most triticale like. Classes 1 and 2, the more wheat-like types, contained the majority of the lines within the population, indicating that a portion of the population is "segregating" towards the wheat seed coat type. Figure 12 illustrates the class types found in the population.

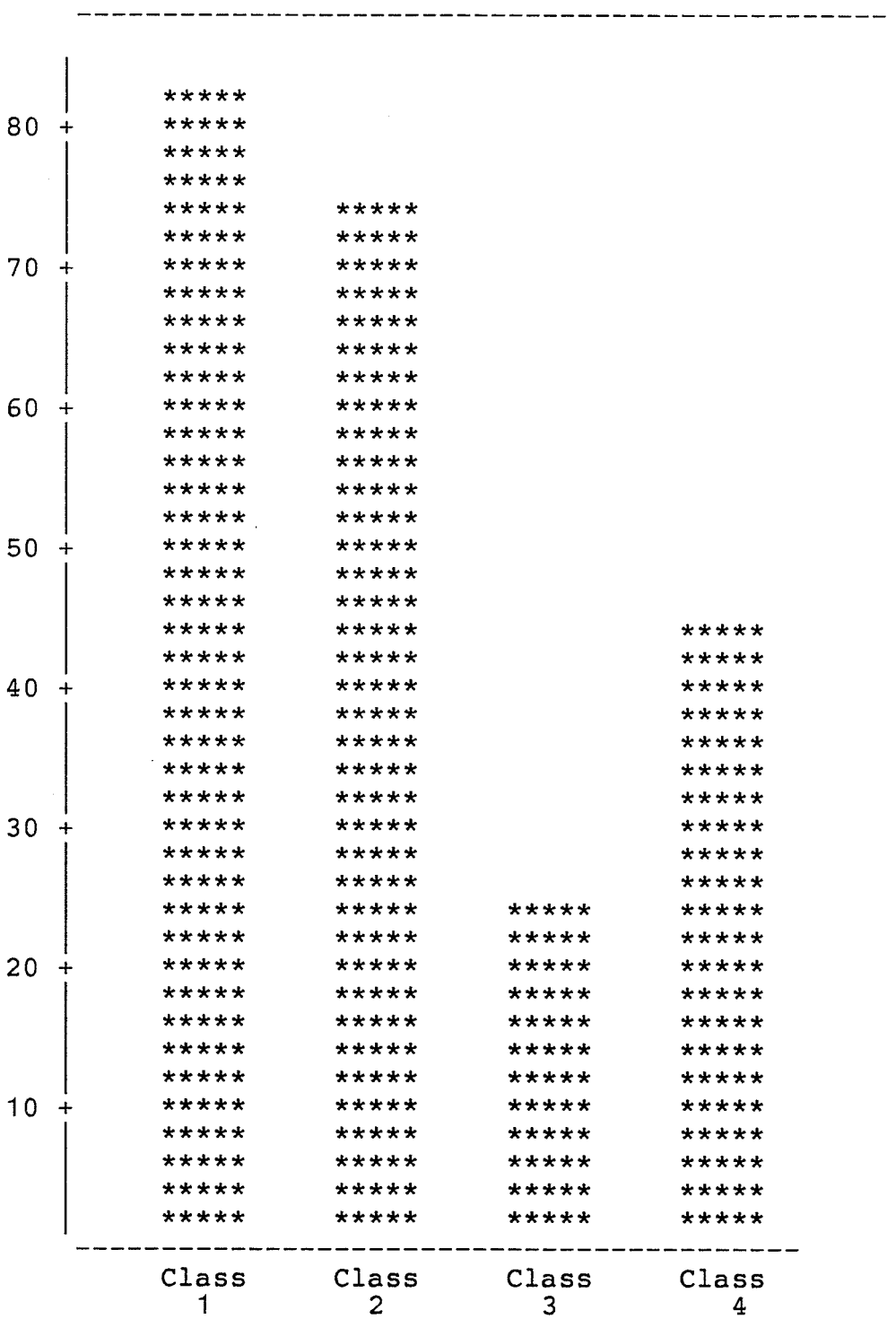

Figure 11. The distribution of kernel appearance of F4 progeny from a cross of 6A250 x Anza grown at the University of Manitoba in 1978.
Class 1=wheat-like, class 4=triticale like.

Figure 12. Illustration of kernel appearance class types into which the F4 progeny from a cross of 6A250 x Anza was divided.

4.5.2 Kernel Shrivelling

The distribution of F4 lines according to their degree of shrivelling was quite different from that for kernel appearance. (Figure 13). Class 1 represents lines with plump, hard kernels; class 4, contains the most shrivelled lines. In the latter class, the majority of lines resemble the triticale parent, 6A250. Class types are illustrated in Figure 14.

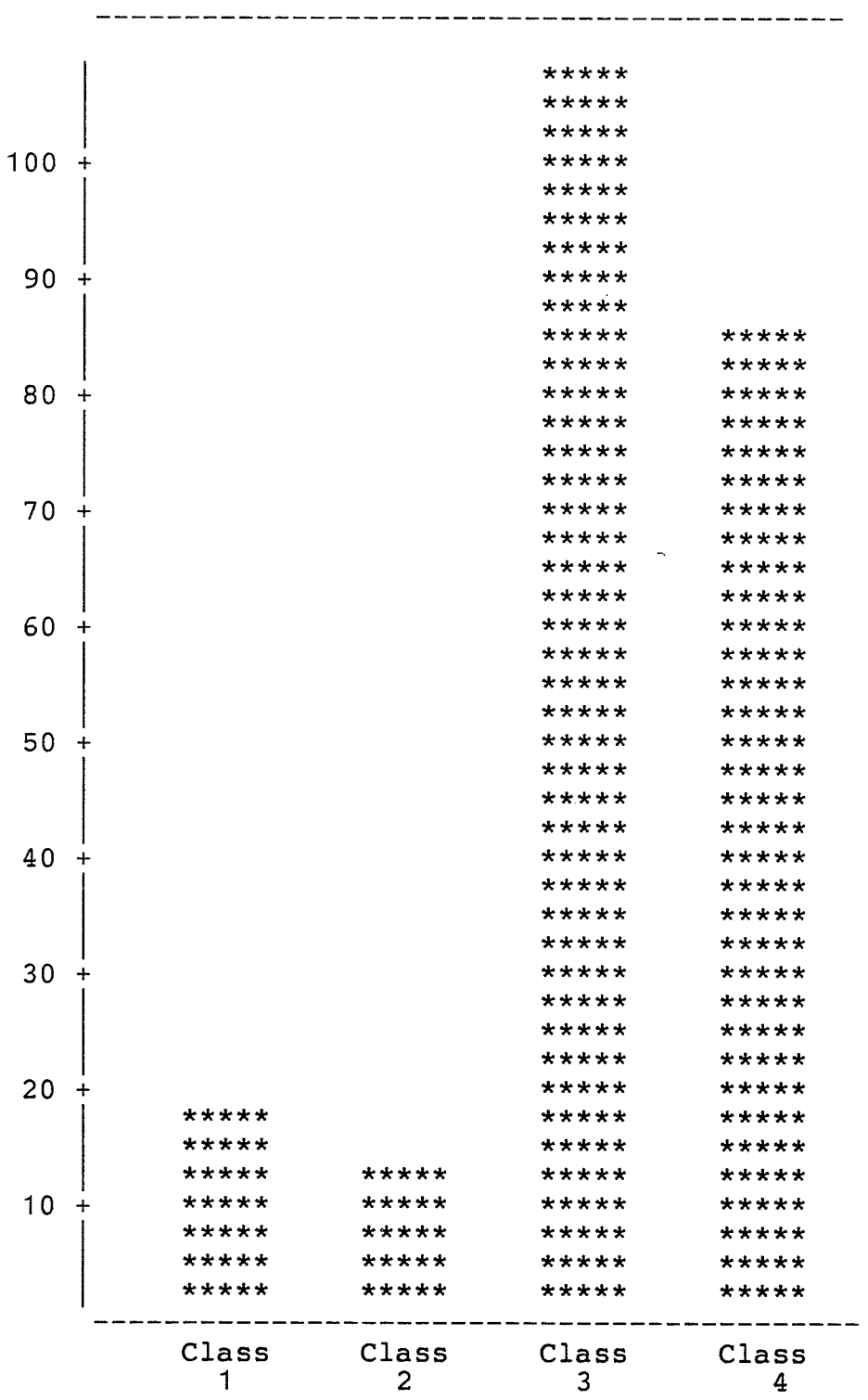

Figure 13. The distribution of F4 progeny from a cross of 6A250 x Anza classified as to the degree of shrivelling of the kernels.
Class 1=plump; class 4=highly shrivelled.

Figure 14. Illustration of shrivelled kernel classes into which the progeny from a cross of 6A250 x Anza was divided.

4.6 FERTILITY

Fertility values for the F5 population grown at the University of Manitoba and at the University of California at Davis are charted in Figures 15-16. (No data were obtained for the F4 in 1978). Location exerted considerable variation on the sites grown in 1979. The mean fertility of the U. of Manitoba population was 2.35 seeds/spikelet compared to a mean of 2.73 at Davis, California. In general, the material grown at Davis was more fertile than when grown at the University of Manitoba, and showed a decreased range of variability.

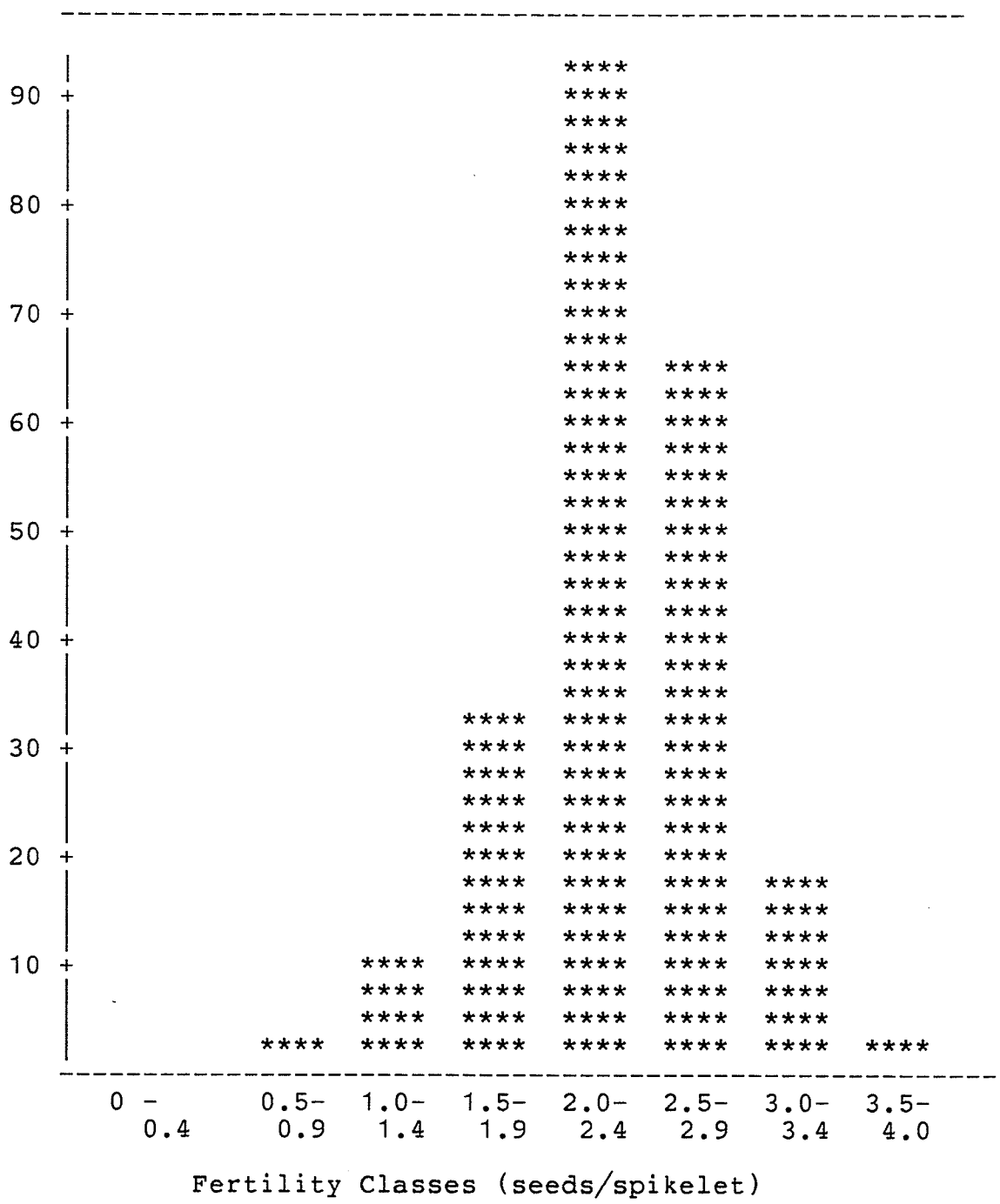

Figure 15. Fertility estimates of F5 progeny from a cross of 6A250 x Anza Grown at the University of Manitoba in 1979.

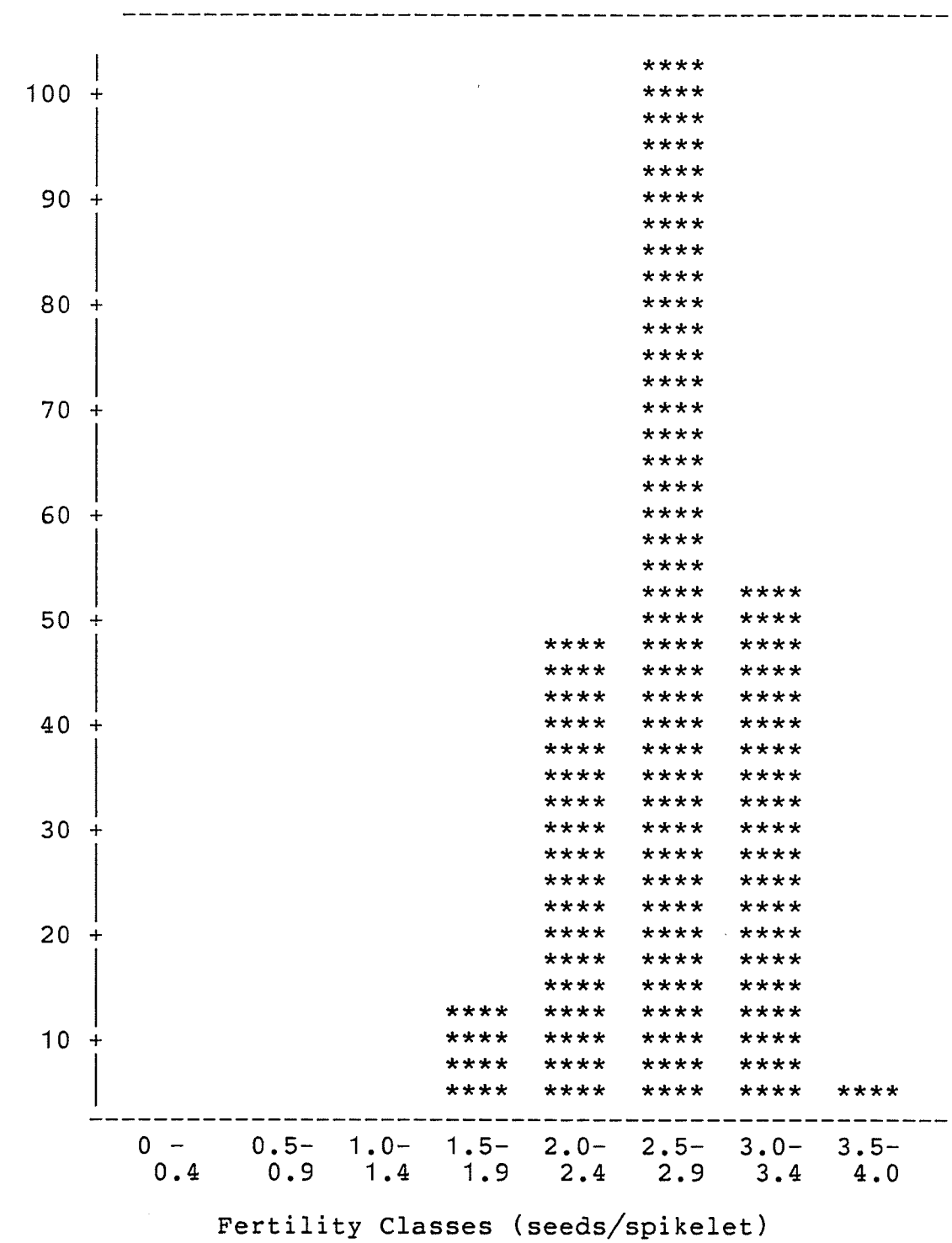

Figure 16. Distribution of fertility assessments of the F5 progeny from a cross of 6A250 x Anza grown at the University of California at Davis, in 1979.

4.6.1 Relationship of Fertility and Protein.

The F5 generation grown at the University of Manitoba and at Davis, California displayed a negative correlation (r=-0.32 and r=-0.25, P=0.001) between total protein and fertility. Similar observations in wheat were made by Clark (1926) and by Campbell and Davidson (1979) who noted that even at non-limiting levels of nitrogen, protein was inversely related to yield (of which seeds/spikelet was a component, r=-0.65**).

In 1979 at the University of Manitoba, fertility and lysine exhibited a low but significant (P=0.001) relationship (r=-0.21). At Davis, the correlation (r=0.05) was not significant.

4.7 DIFFERENTIAL ELIMINATION OF RYE CHROMOSOMES

Figure 17 illustrates the frequency with which rye chromosomes appeared in the lines examined. Chromosome 1R occurred most frequently whereas chromosome 2R appeared only in those lines containing a complete complement of rye chromosomes. This non-random occurrence of particular rye chromosomes is typical of the findings of others (Gustafson, 1976; Gustafson and Bennett, 1976; Sowa and Gustafson, 1980; Gustafson and Zillinsky, 1978; Merker, 1975).

The findings involving the present F4 generation are also of interest in comparison with a study conducted on the F3 generation of the same population (Sowa and Gustafson,

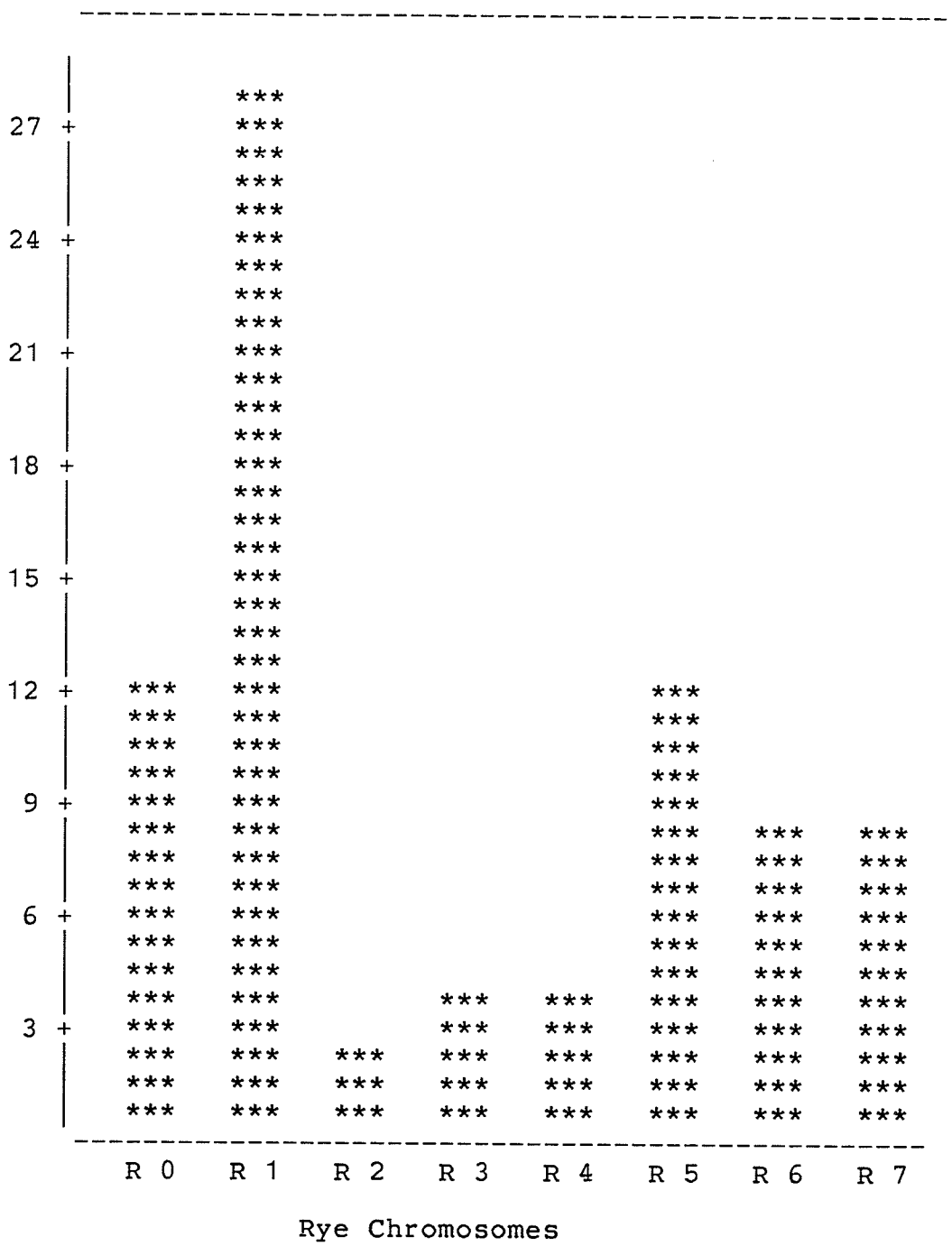

Figure 17. Frequency of occurrence of rye chromosomes in the F4 progeny from a cross of 6A250 x Anza.

1980). Between F3 and F4, the frequency of appearance of all rye chromosomes decreased (Table 5). Some chromosomes notably 1R and 2R maintained their relative rank as the most frequent and least frequent while other rye chromosomes did not. The elimination of rye chromosomes from the population as illustrated in Figure 17 and Table 5 is not random: both

Table 5. Comparison of rye chromosomes present in the F3 and F4 progeny of a cross of 6A250 x Anza.

F4 Generation		F3 Generation*	
	% of population		% of population
**0R	37	0R	0
1R	59	1R	100
5R	40	4R	77
7R	28	6R	73
6R	28	3R	70
3R	19	5R	60
4R	15	7R	50
2R	9	2R	3

*F3 data from Sowa and Gustafson, 1980.
**0R = no rye chromosomes present.

genetic and nucleotypic factors are assumed to be involved.

The A, B, and D genomes of tetraploid and hexaploid wheats are known to be adapted for co-existence in the nucleus. The recently introduced R genome has not yet undergone that evolution for co-adaptation with the wheat genome. Thus, it is possible that natural selection would result in

the loss of those rye chromosomes that confer little or no selective advantage to the organism. In their place would be a substitution by a homoeologous chromosome from the wheat genome.

The large dense segments of telomeric heterochromatin of rye chromosomes are thought to contribute to the meiotic instability observed in triticale (Bennett, 1973; Gustafson and Bennett, 1976; Gustafson and Zillinsky, 1978). The late replicating nature of these rye segments relative to the wheat genome causes late disjunction at meiosis and ultimately the loss of the entire rye chromosome. Lima de Faria and Jaworska, (1972) noted that all chromosomes started replication synchronously in S phase, but the time required to complete replication was directly related to the size of the chromosome. Thus, the chromosomes having the largest amount of DNA would require the longest time to replicate and be most likely to be the first to be lost. Gustafson & Bennett (1976) estimated the size of rye chromosomes and ranked them in descending order as: 2R, 7R, 6R, 4R, 3R, 5R, and 1R. From this, 2R would be expected to be first lost and 1R the last. This assumption was verified from the present results. From other studies, it has been shown that chromosome 2R is consistently eliminated early from wheat and rye populations (Gustafson et al. 1984). For example, the triticale cultivar "Armadillo" was found to have a 2D(2R) substitution (Gustafson and Zillinsky, 1973) as did most of the

CIMMYT triticale lines investigated (Merker, 1975) during the 1970's.

Riley (1960) added four disomic rye chromosomes to hexaploid wheat and found that those containing 2R suffered the more severe meiotic disturbance and depression of fertility. As well, bivalents 2R and 3R tended to be asynaptic and seemed to cause an increase in the frequency of asynapsis within the wheat chromosome complement.

Pieritz (1970) found in two octoploid triticales that 2R either tended to be absent or involved as a supernumerary chromosome twice as often as would be expected by chance and about 10% more often than any other rye chromosome.

Work conducted on the triticale cultivar Rosner could not identify 2R as being present (Merker, 1975). Later, Gustafson et al., (1984) confirmed that 2R was absent, but it was not possible to identify the substituting chromosome as being 2D. Gustafson and Bennett (1976) suggested that the loss of the late replicating heterochromatic telomeres would reduce 2R to the relative size of the B genome of wheat making it more compatible with the wheat genome. It is also possible that the natural advantage of the 2D/29R substitution in daylength insensitive populations may be responsible, as Gustafson et al.,(1984) noted that in daylength sensitive populations the 2D for 2R substitution occurred with only the third highest frequency.

4.7.1 Rye chromosomes other than 2R

Relative to 2R, the remainder of the rye chromosomes in the F3 population were more random in the frequency of their elimination (Gustafson and Zillinsky, 1978). A generation later, in the F4, the pattern of chromosome substitution was changing from that seen in the F3. Gustafson et al., (1984) found a correlation of r=-0.78 between chromosome length of rye chromosomes and the frequency of elimination, but when 2R was removed from the calculations the correlation was no longer significant (Gustafson et al., 1984). In the F4, chromosomes 1R and 2R remained as the most and least frequently occurring rye chromosomes, respectively, but at reduced frequencies as were all rye chromosomes. A total of 37% of the lines examined showed no identifiable rye chromosomes. In the F3, 1R appeared in all of the plants examined (Sowa and Gustafson, 1980). In the F4, 1R was present in only 59% of the lines examined. Chromosome 5R which ranked next most frequent to 1R, was present 40% of the time in the F4 generation vs 60% and only fourth most frequent in the F3. Chromosomes 6R and 7R have similar DNA content (Gustafson and Bennett, 1976) and both appeared in 28% of the lines examined in the F4 as compared to 70% and 60% respectively, in the F3 population. Chromosomes 3R and 4R are also similar in DNA content and appear in 19% and 15% of the F4 lines respectively. In the F3 generation 3R and 4R appear in 70% and 77% of the lines, respectively. Based on DNA content alone, one would expect 3R and 4R to appear more frequently

than 6R and 7R. Merker (1975) found that 6R occurred most frequently in the selection of lines examined from the CIMMYT program followed closely by 1R. His material was different from the current study in that the CIMMYT lines had undergone intensive breeder selection for good agronomic characters which would probably tend to differentially eliminate certain of the substitutions. In the present study, no human selection was applied to the populations throughout the series of generations.

4.8 PROTEIN CONTENT AND CHROMOSOMAL ASSOCIATIONS

Protein values were not found to be strongly associated with a particular rye chromosome in the present study, although 60% of those having more than 17% protein possessed chromosome 5R. Chromosome 1R is present in all classes, although it tended to be absent from the very low protein class The findings of Jagannath and Bhatia (1972) and Law et al., (1972), in which the substitution of chromosome 2R for its homoeologues in wheat was associated with higher protein content were not duplicated in the present study. The two lines containing chromosome 2R displayed low protein levels. (Table 6).

The middle range of protein values (15-17%), those better than the parent Anza, consisted of plants having three, four, or more rye chromosomes. Also present were those having only chromosome 1R or an absence of rye chromosomes.

Table 6. Relationship between protein content in F4 plants from a cross of 6A250 x Anza and the presence of specific rye chromosomes.

Line Number	Rye Chromosomes Present	Protein Class
20248	1	
20562	1,5,7	
20573	1,4,5	High Protein
*20606	mod. 1,5	Lines
*21021	mod. 1,4,5 (41')	(17%+)
20933	1,6	
21043	1,5	
21842	7	
21504	0	
20098	1,3,5,6,7	
20247	0	Midlevel Protein
20419	1,5,6	Class
20430	1,4,5,6	(15-17%)
20437	0	
20661	1	
20664	1	
20804	1,3,5,6,7	
20844	0	
20017	1	
20059	0	
20175	0	
20207	0	Low-level Protein
20244	0	Class
20156	1,2,3,4,5,6,7	(below 15%)
20330	1	
20246	0	
20603	0	
20667	7	
20704	0	
21503	0	
21862	1,3,5,6,7	
21869	1,2,3,5,6,7	

* Chromosome 1R carries a partial deletion of the heterochromatic band on one telomere.
41' indicates that the plant is monosomic for an unknown wheat chromosome.

Some of these types may be exhibiting the deletions discussed by Gustafson et al., (1984) whereby the heterochromatic telomere of a rye chromosome is deleted, making it difficult to discern it from a wheat chromosome. Some lines in this study which are classed as having no rye chromosomes, for example line 20844, but which has protein levels of 16.4%, would indicate that some rye genome material is present, either as a whole chromosome lacking telomeres or as a translocation of the type found by Gustafson et al., (1983).

In the F3 generation of material from the cross 6A250 x Anza, Sowa and Gustafson (1980) found that the majority of the high protein lines had four or more pairs of rye chromosomes. In the present study of the F4 generation, no plant having more than 17% protein contained more than three rye chromosomes. In comparison with the F3 in which lines with a complete or nearly complete rye genome tended to have higher protein, lines in F4 tended to be found in the low to mid-protein classes. Such a difference in one generation could possibly be due simply to chance - a result of sampling error from a large, diverse population.

4.9 LYSINE CONTENT AND CHROMOSOME ASSOCIATION

The rye genome composition of lysine classes is the converse of the total protein profile. High lysine lines have three or more rye chromosomes, whereas with one exception, lines in the low lysine class have either 1R or 7R or no rye chromosomes (Table 7).

Riley and Ewart (1970) found an eight percent increase in lysine content of wheats to which chromosome 5R was added. In the present study, chromosome 5R was present in all high lysine lines, although it appeared in other classes as well. Chromosomes 2R and 3R were strongly associated with high lysine content. These chromosomes were also associated with depressed total protein. They may be acting to promote high lysine at the expense of total protein content. In the mid level lysine class, there is a variable number of different rye chromosomes.

In the lines identified, those having high lysine contained superior, moderate or low total protein values in about equal frequencies. Of interest for breeding possibilities are the two lines 21021 and 20606 which both contain a modified telomere on chromosome 1R. Both lines exhibit higher lysine content combined with good to superior protein levels.

Table 7. Average percent lysine content of the F4 and F5 progeny of a cross of 6A250 x Anza, and rye chromosome association.

Line Number	Rye Chromosomes Present	Lysine Class
20098	1,3,5,6,7	
20156	1,2,3,4,5,6,7	
20419	1,5,6	High Lysine
20804	1,3,5,6,7	(3.3%+)
*21021	mod. 1,4,5 (41')	
21862	1,3,5,6,7	
21869	1,2,3,5,6,7	
20017	1	
20059	0	
20244	0	
20246	0	
20330	1	Mid-level Lysine
20430	1,4,5,6	(2.95-3.3%)
20437	0	
20573	1,4,5	
*20606	mod. 1,5	
20661	1	
20664	1	
20667	7	
20704	0	
20933	1,6	
21043	1,5	
20175	0	
20207	0	
20247	0	
20248	1	Low Lysine
20562	1,5,7	(below 2.95)
20603	0	
20844	0	
21503	0	
21504	0	
21842	7	

* Contains a chromosome 1R which carries a deletion for a portion of the heterochromatic telomere.
41' indicates that the plant is monosomic for an unknown wheat chomosome.

4.10 KERNEL TYPE AND CHROMOSOME ASSOCIATION

4.10.1 Kernel Appearance

Table 8 illustrates classes into which the identified lines were divided into on the basis of seed coat appearance and color.

The wheat like class of kernels appear to be largely associated with the absence of rye chromosomes, with identifiable rye chromosomes being absent from over 50% of the class. Chromosome 1R is the only rye chromosome common in the class. A total of 76% of the lines in the wheat-like class either lacked rye chromosomes or contained 1R alone. In the remainder of the class, two or three of 1R, 4R, 5R, 6R or 7R appeared in combination. Merker (1975) found a line containing 1R and 6R whose kernels were like bread wheat, but shrivelled. Line 20933 was found to verify that observation as well. Chromosomes 2R and 3R do not appear in the wheat-like kernel class, but are associated with the triticale-like kernels class.

In the triticale-like kernel class over 50% of the lines have four or more rye chromosomes. This is in agreement with other work done on the same population (Gustafson and Zillinsky, 1978; Sowa and Gustafson, 1980; Gustafson, 1982; Gustafson et al., 1984). Merker (1975) also found plump wheat-like kernels to be associated with fewer rye chromosomes. Approximately 45% of the triticale-like class however, have three or fewer rye chromosomes. Sowa and Gustaf-

Table 8. Kernel appearance of the F4 progeny from a cross of 6A250 x Anza and rye chromosome association.

Line Number	Rye Chromosomes Present	Kernel Type
20017	1	
20059	0	
20175	0	
20207	0	Wheat-like
20244	0	
20246	0	(rated 1-2)
20247	0	
20248	1	
20437	0	
20562	1,5,7	
20573	1,4,5	
20603	0	
20661	1	
20664	1	
20667	7	
20704	0	
20844	0	
20933	1,6	
21043	1,5	
21503	0	
21504	0	
20098	1,3,5,6,7	
20156	1,2,3,4,5,6,7	
20330	1	Triticale-like
20419	1,5,6	
20430	1,4,5,6	(rated 3-4)
*20606	mod. 1,5	
20804	1,3,5,6,7	
*21021	mod. 1,4,5 (41')	
21842	7	
21862	1,3,5,6,7	
21869	1,2,3,5,6,7	

* Contains a modified chromosome 1R which carries a partial heterochromatic telomere.
41' indicates that the plant is monosomic for an unknown wheat chromosome.

Table 9. Kernel shrivelling of the F4 progeny from a cross of 6A250 x Anza and rye chromosome association.

Line Number	Rye Chromosomes Present	Degree of Shrivelling
20419	1,5,6	
20430	1,4,5,6	
*20606	mod. 1,5	
20804	1,3,5,6,7	
20933	1,6	
21842	7	
20017	1	
20059	0	
20098	1,3,5,6,7	High
20244	0	Shrivelling
20246	0	
20248	1	(rated 3-4)
20437	0	
20661	1	
20667	7	
20844	0	
*21021	mod. 1,4,5 (41')	
21043	1,5	
21503	0	
21504	0	
21862	1,3,5,6,7	
20175	0	
20207	0	
20247	0	
20330	1	Low Shrivelling
20562	1,5,7	
20664	1	(rated 1-2)
20573	1,4,5	
21869	1,2,3,5,6,7	
20156	1,2,3,4,5,6,7	
20603	0	
20704	0	

* Contains a chromosome 1R which carries a deletion for a portion of the heterochromatic telomere.
41' indicates that the plant is monosomic for an unknown wheat chromosome.

son, (1980) found 7R, 6R and 3R to be associated with triticale- like kernels. The present material supports that observation although the distinction between classes has become less marked between the F3 and F4 generations.

Merker (1975), in an examination of some CIMMYT substitution lines, found that chromosomes B and F (3R and 5R) greatly influenced the triticale morphology of the plant. He suggested that suppression of rye characters by the wheat genome, may account for this behaviour and cited the expression of the "hairy neck" gene carried by 5R. In the progeny of selections made from Camel-Pato crosses the range of expression included extremes from smooth to heavily haired peduncles. The same chromosomal composition was contained by all plants, but reached different levels of expression.

As has been observed, (Gustafson et al., 1984) substitutions of the D genome may occur for members of the A or B genome as well as the R, and this would alter the chromosome constitution of the lines.

4.10.2 Shrivelling and Chromosome Association

Sowa and Gustafson (1980) found in the F3 generation of the present material that kernel shrivelling was generally associated with chromosomes 7R, 6R and 3R; and that wheat-like kernels lacked 7R. In the present F4 generation, rye chromosomes are distributed approximately equally between the two classes and no strong associations were apparent. In

the previous generation, Sowa and Gustafson (1980) also noted the variability of rye chromosomes present in the classes, particularly with regard to chromosome 5R.

Kaltsikes and Roupakias (1975) and Darvey (1973) noted that 5R, 4R, 6R and 1R, (in descending order of magnitude) caused an increase in the frequencies of aberrant nuclei per ovule when these chromosomes were added to wheat. The findings of the present study did not associate any particular rye chromosome more strongly than another with kernel shrivelling. However, the material of the present study is composed of a variable group of substitutions versus the additions to wheat as in the aforementioned studies. The effect of a rye chromosome in a background of substitutions may depend heavily on the composition of the wheat genome for its expression, as in the hairy neck character cited. Further evidence is presented by Darvey (1973) who found that 5R when substituted for wheat chromosome 5A or 5B, shrivelling was unaffected, whereas when added to wheat it caused shrivelling. Differences in the data would support the idea that shrivelling can be the result of several factors. For example, Kaltsikes and Roupakias (1975) found that although 6R produced few aberrant nuclei, shrivelling still occurred.

4.11 FERTILITY

In the present study, all rye chromosomes seem to be associated with depressed fertility (Table 10). One exception, line 20562 containing chromosomes 1R, 5R and 7R, appears in the high fertility class. The mid-level fertility class contains a significant number of lines with no identifiable rye chromosomes. These lines may be suspected of carrying rye chromosomes which have undergone deletions of heterochromtic bands which makes them impossible to identify with the technique used. Lines containing 2R are all associated with low fertility. This rye chromosome was found to be absent in the high yielding triticale variety "Armadillo" (Gustafson and Zillinsky, 1973). Riley (1960) also found that 2R when added to wheat resulted in meiotic instability and low fertility in a series of disomic rye addition lines examined.

Table 10. Fertility of the F5 progeny from a cross of 6A250 x Anza and rye chromosome association.

Line Number	Rye Chromosome Present	Fertility
20059	0	
20244	0	
20246	0	High Fertility
20437	0	>2.8
20562	1,5,7	seeds/spikelet
21504	0	
20175	0	
20207	0	
20247	0	
20248	1	
20330	1	Mid-level
20419	1,5,6	Fertility
20430	1,4,5,6	
20573	1,4,5	2.25-2.8
20603	0	seeds/spikelet
20661	1	
20664	1,	
20667	7	
20704	0	
20804	1,3,5,6,7	
20844	0	
21043	1,5	
21503	0	
21862	1,3,5,6,7	
20017	1	
20098	1,3,5,6,7	
20156	1,2,3,4,5,6,7	Low Fertility
*20606	mod. 1,5	1.0-2.25
*21021	mod. 1,4,5 (41')	seeds/spikelet
20933	1,6	
21842	7	
21869	1,2,3,5,6,7	

* Contains chromosome 1R which carries a partial heterochromatic telomere.
41' indicates that the line is monosomic for some unknown wheat chromosome.

4.12 KERNEL WEIGHT

Generally, lines containing no identifiable rye chromosomes were associated with mid-range and low kernel weights. The high kernel weight class was largely composed of lines containing rye chromosomes (Table 11). In the higher kernel weight class (30+ grams), 70% of the lines contain three or more rye chromosomes. Chromosome 5R predominates in the high kernel weight class, although it occurs in the other classes as well. Sowa and Gustafson (1980) found in the F3 generation that chromosome 4R was most associated with kernel weight. In the present study however, 4R occurred too infrequently to permit a conclusion to be reached.

Table 11. Kernel weight of the F4 progeny from a cross of 6A250 x Anza and rye chromosome association.

Line Number	Rye Chromosomes	Kernel Weight
20330	1	
21503	0	Low
20419	1,5,6	0 to
20430	1,4,5,6	25 g.
20603	0	
*20606	1,5	
20704	0	
21842	7	
21504	0	
20017	1	
20059	0	
20098	1,3,5,6,7	Mid-range
20244	0	Kernel Weight
20246	0	25-30 g.
20247	0	
20248	1	
20437	0	
20661	1	
20664	1	
20667	7	
20844	0	
21043	1,5	
21862	1,3,5,6,7	
21869	1,2,3,5,6,7	
20156	1,2,3,4,5,6,7	High Kernel
20175	0	Weight
20207	0	
20562	1,5,7	30+ g.
20573	1,4,5	
20804	1,3,5,6,7	
20933	1,6	
*21021	1,4,5 (41')	

* Contains chromosome 1R which carries a partial heterochromatic telomere.
41' indicates that the line is monosomic for some unknown wheat chromosome.

Chapter V

CONCLUSIONS

The study reported in this thesis involved the comparative evaluation of specific agronomic, grain quality, and cytogenetic traits in successive unselected generations of hybrids derived from a secondary triticale of genomic constitution, AABBD(R). Because of the unsynapsed chromosomes of the D and R genomes of wheat and rye, respectively, it was possible to relate various plant traits to the presence or absence of specific rye (R) chromosomes as identified by the C-banding technique. The following observations were made:

1. The intergeneration loss of rye chromosomes occurred in the descending order of frequency of 2R, 4R, 3R, 6R, 7R, 5R and 1R. Hypotheses governing chromosome elimination were discussed.

2. Rye chromosome 5R was found to be associated with high protein while chromosome 2R, and to a lesser extent, 3R, were strongly associated with depressed total protein levels. These three chromosomes were also strongly associated with high lysine content. Lines 20933, 20606 and 21043 identified as high percent total protein combined with moderate to high lysine are potential breeding material in which the commonly observed phenomena of decreasing lysine with increasing protein is transcended.

3. The degree of shrivelling of the grain could not be associated with any individual rye chromosomes. It was noted that lines in the population containing no identifiable rye chromosomes were frequently found to have shrivelled grain. Two lines, 20562 and 20573 listed as high protein types were also found to have plump kernels. Line 20573 has further superior qualities in possessing moderately high lysine content.

4. High fertility was associated generally with the absence of rye chromosomes. No individual rye chromosomes seemed to be associated with fertility levels, although a greater number of lines (50%) in the low fertility class had three or more rye chromosomes than in the mid-level fertility class (27%). Line 20562 was found to be one of the most fertile lines for which chromosomal analysis was done.

5. High thousand kernel weight was generally associated with lines having three or more rye chromosomes. The superior lines 20562 and 20573 are found in the high kernel weight class (>30 g). Of the high protein and lysine lines mentioned, 20933 was identified as possessing high kernel weight.

6. Not examined in this study is the probability that some translocations and/or modifications (deletions of heterochromatic terminal bands) have taken place in the material studied. Several lines displayed protein or lysine lev-

els superior to the parent Anza, and yet no apparent rye chromosomes were found. These may be suspected translocations or deletions of heterochromatic terminal bands.

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