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9. ABSTRACT

Inheritance of grain protein and lysine in three wheat crosses involving high-protein parents was investigated. Three high-protein wheats, April Bearded (C.I. 7337), Atlas 66 (C.I. 12561), and Nap Hal (P.I. 176217) were crossed in diallel fashion without reciprocals. Spaced plants of the parents, F_1, F_2, and backcross populations for each cross were grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Phenotypic correlations of protein and lysine with several traits were made. Generally, negative and significant correlations were found between protein and plant yield and protein and kernel weight. The correlations existed in nonsegregating as well as segregating populations. The magnitude of the correlations was highly variable with most being less than -0.50. Protein content increased as shriveling increased within nonsegregating and segregating populations.

Protein content was inversely related to lysine (percent of protein). Correlations between protein and lysine percent on a dry weight basis were positive and significant. Small inconsistent correlations were detected between lysine (percent of protein) and plant yield, kernel weight, kernel size, and shriveling.

Mean phenotypic performance of genotypes was inconsistent for protein and lysine across locations. Genotype by location interactions were highly significant for protein and lysine.

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INHERITANCE OF GRAIN PROTEIN AND LYSINE IN CROSSES OF THREE HIGH-PROTEIN WHEATS (TRITICUM AESTIVUM L.)

by

Allen L. Diehl

A DISSERTATION

Presented to the Faculty of
The Graduate College in the University of Nebraska
In Partial Fulfillment of Requirements
For the Degree of Doctor of Philosophy

Department of Agronomy

Under the Supervision of Dr. V. A. Johnson

Lincoln, Nebraska

August, 1974

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TABLE OF CONTENTS

	Page
LIST OF TABLES	iii
LIST OF FIGURES	vii
INTRODUCTION	1
LITERATURE REVIEW	3
The Protein Problem and Improvement by Plant Breeding	3
Wheat Kernel Proteins and Kernel Morphology	5
Protein and Lysine Relationships	6
Environmental Influences on Protein and Lysine	7
Breeding for High Protein and High Lysine Content in Wheat	8
MATERIALS AND METHODS	13
Genetic Materials	13
Locations	14
Experimental Design and Procedure	17
Traits Measured	18
Statistical Analyses	19
Genetic Analyses	20
EXPERIMENTAL RESULTS	23
Protein	23
Lysine	28
Population Variances	29
Genotype-Environment Interaction	34
Correlated Responses	34
Protein	34
Lysine	38
Gene Effects	40
Protein	40
Lysine	42
Heritability	44
DISCUSSION	47
SUMMARY	55
LITERATURE CITED	57
APPENDIX	62

TABLE OF TABLES

Page

Table 1. Populations, generations, abbreviations, and the number of rows per replication utilized in this study 15

Table 2. Means and LSD's of measured traits for 15 genotypic means in four replications at Yuma, Arizona in 1973 24

Table 3. Means and LSD's of measured traits for 15 genotypic means in four replications at Fort Collins, Colorado in 1973 25

Table 4. Means, standard deviations, and coefficients of variation of measured traits for sixteen Lerma Rojo border plants grown at Yuma, Arizona and Fort Collins, Colorado in 1973 26

Table 5. Between plant variances within populations for protein percent and lysine as a percent of protein in 15 genotypic populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973 32

Table 6. F values to test for equal variances of protein and lysine between F_1 and F_2 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973 33

Table 7. Combined analyses of variance (fixed model) over locations for protein and lysine as a percent protein 35

Table 8. Phenotypic correlations between protein and other traits measured on individual plants of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973 36

Table 9. Phenotypic correlations between lysine as a percent protein and other traits measured on individual plants of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973 39

Table 10. Estimates of genetic effects and their standard errors by the weighted three-parameter and six-parameter models for protein in three wheat crosses grown at Yuma, Arizona and Fort Collins, Colorado in 1973 41

TABLE OF TABLES (Cont.)

Page

Table 11. Estimates of genetic effects and their standard errors by the weighted three-parameter and six-parameter models for lysine as a percent of protein in three wheat crosses grown at Yuma, Arizona and Fort Collins, Colorado in 1973 43

Table 12. Heritability estimates of protein and lysine as a percent of protein for three crosses grown at Yuma, Arizona and Fort Collins, Colorado in 1973 . 45

TABLE OF APPENDIX TABLES

Page

Table A1. Means, variances, ranges, and coefficients of variation for percent grain protein of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 63

Table A2. Means, variances, ranges, and coefficients of variation for lysine as a percent of protein of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 64

Table A3. Means, variances, ranges, and coefficients of variation for adjusted lysine percent of protein of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 65

Table A4. Means, variances, ranges, and coefficients of variation for lysine percent on a dry weight basis of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 66

Table A5. Means, variances, ranges, and coefficients of variation for yield per plant of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 67

Table A6. Means, variances, ranges, and coefficients of variation for kernel weight of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 68

Table A7. Means, variances, ranges, and coefficients of variation for plant height of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 69

TABLE OF APPENDIX TABLES (Cont.)

Page

Table A8. Means, variances, ranges, and coefficients of variation for shrivel index of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado. Statistics based on individual plant data grouped across replications and plots to form one sample . 70

Table A9. Means, variances, ranges, and coefficients of variation for kernel size for 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 71

Table A10. Means, variances, ranges, and coefficients of variation for shrivel type of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 72

Table A11. Means, variances, ranges and coefficients of variation for shrivel frequency of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample 73

Table A12. Analyses of variance of measured traits based on generation means grown at Yuma, Arizona and Fort Collins, Colorado in 1973 74

Table A13. Nested analyses of variance to determine between plant variance of protein and lysine as a percent of protein for 15 populations grown at Yuma, Arizona in 1973 75

Table A14. Nested analyses of variance to determine between plant variance of protein and lysine as a percent of protein for 15 populations grown at Fort Collins, Colorado in 1973 76

TABLE OF FIGURES

Page

Figure 1. Linear relationship of lysine as a percent of protein with protein for April Bearded, Atlas 66, Nap Hal, and Lerma Rojo grown at Yuma, Arizona in 1973 30

Figure 2. Linear relationship of lysine as a percent of protein with protein for April Bearded, Atlas 66, Nap Hal, and Lerma Rojo grown at Fort Collins, Colorado in 1973 31

INHERITANCE OF GRAIN PROTEIN AND LYSINE

IN CROSSES OF THREE HIGH-PROTEIN WHEATS (TRITICUM AESTIVUM L.)

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University of Nebraska, 1974

Advisor: Dr. V. A. Johnson

Inheritance of grain protein and lysine in three wheat crosses involving high-protein parents was investigated. Three high-protein wheats, April Bearded (C.I. 7337), Atlas 66 (C.I. 12561), and Nap Hal (P.I. 176217) were crossed in diallel fashion without reciprocals. Spaced plants of the parents, F_1, F_2, and backcross populations for each cross were grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Phenotypic correlations of protein and lysine with several traits were made. Generally, negative and significant correlations were found between protein and plant yield and protein and kernel weight. The correlations existed in nonsegregating as well as segregating populations. The magnitude of the correlations was highly variable with most being less than -0.50. Protein content increased as shriveling increased within nonsegregating and segregating populations.

Protein content was inversely related to lysine (percent of protein). Correlations between protein and lysine percent on a dry weight basis were positive and significant. Small inconsistent correlations were detected between lysine (percent of protein) and plant yield, kernel weight, kernel size, and shriveling.

Mean phenotypic performance of genotypes was inconsistent for protein and lysine across locations. Genotype by location interactions were highly significant for protein and lysine.

Grain protein of Nap Hal was significantly higher than April Bearded and Atlas 66 at Yuma. The protein levels of April Bearded and Atlas 66 were not statistically different at this location. At Fort Collins, Atlas 66 grain protein was about four percentage points higher than grain protein of April Bearded and Nap Hal. No statistical differences were found between April Bearded and Nap Hal at Fort Collins.

Lysine content (percent of protein) of the parents was highest for Nap Hal at both locations. Its average lysine content was 3.05%. At Yuma, lysine content of Nap Hal was significantly greater than the other two parents but at Fort Collins Nap Hal was only significantly better than Atlas 66. April Bearded possessed significantly higher lysine levels than Atlas 66 at both locations.

Protein means of F_1 hybrids were always below mid-parent values, near the low-protein parent, or below the low-protein parent. Protein may have been influenced by heterosis for plant yield. Lysine means of the F_1 generations tended to be near mid-parent values.

Examination of generation means and between plant variances suggests that Atlas 66, April Bearded, and Nap Hal possess different genes for high protein. Genes for high protein from Atlas 66 were expressed over environments but genes from Nap Hal and April Bearded were not stable in phenotypic expression. April Bearded and Nap Hal have high-protein genes in common but minor gene differences probably exist.

Expression of high-lysine genes over environments was relatively stable. High-lysine genes from April Bearded and Nap Hal are probably different, although both may possess some common genes.

Heritability estimates in the narrow and broad sense were positive for the April Bearded/Nap Hal population at each location. Estimates at

Fort Collins were also positive for April Bearded/Atlas 66 and Atlas 66/Nap Hal. Negative or low positive estimates were found for the latter two crosses at Yuma.

Gene effects as described by Hayman's model indicated that additive, dominance, and epistasis types of gene action existed for protein and lysine inheritance in these crosses. High protein and high lysine probably are due to the accumulation of favorable recessive genes.

INTRODUCTION

It has been estimated that cereals account for approximately 50% of the proteins consumed by the world's human population (Kent, 1970). Human requirements for pure protein are projected to be 69 million tons in 1975. By the year 2000, an increase of 57% will be needed to meet projected requirements of 108 million tons. An additional 150-200 million tons per year will be required for animal feed (Milling and Baking News, 1973).

Increased protein content in the cereal grains could aid in alleviating the protein problem. Average protein percent of wheat is 14.3%; rye, 13.4%; corn, 10.2%; barley, 13.0%; oats, 12.0%; rice, 9.2%; and sorghum, 12.5% (Shellenberger, 1971). Protein values within a cereal do vary; for instance, wheat protein content can vary from 7% to 22% (Shellenberger, 1971). This variability can be attributed to genetic and environmental influences.

Eight essential amino acids are required by adults. They are lysine, tryptophan, phenylalanine, methionine, leucine, isoleucine, threonine, and valine (Nelson, 1969). Essential amino acids cannot be synthesized by man or monogastric animals. They must be consumed as free amino acids or as components of protein. A balanced diet of amino acids is important because growth is limited by the amino acid shortest in supply. Storage proteins in wheat as well as those of rice, millet, barley, sorghum, rye, and oats are deficient in the amino acid lysine

(Nelson, 1969). Corn protein is deficient in lysine and tryptophan (Nelson, 1969; Schuphan, 1970). Cereal proteins would be equivalent to milk protein casein if sufficient quantities of lysine plus the second limiting amino acid could be incorporated (Nelson, 1969).

Genetic sources of high protein and high lysine content are being investigated. Researchers at the University of Nebraska have screened the common wheats in the USDA World Wheat Collection for high protein and high lysine content. Three wheats were identified as genetic sources of high protein. They are April Bearded (C.I. 7337), Atlas 66 (C.I. 12561), and Nap Hal (P.I. 176217). Higher than normal lysine levels also have been measured in April Bearded and Nap Hal. This research was conducted to determine if genetic differences for protein and lysine content do exist in these wheats and to elucidate the inheritance of protein and lysine content in crosses of these wheats.

LITERATURE REVIEW

The Protein Problem and Improvement by Plant Breeding

Improvement of quantity and quality of plant proteins warrants investigation due to world population growth and protein-calorie malnutrition. Based on current rates of population growth, projected increases of food requirements in food deficient countries such as India will more than double within the next fifteen years (Bennett, 1968). World population in 1950 was estimated at 2406 million people. Projections on current population growth rates estimate world population could be 6280 million people in 2000--150% increase above 1950 (Leonard and Martin, 1963).

The most efficient means of increasing the amount of available protein in a food is by completing its amino acid profile (Altschul, 1971). Janson (1969) fed rats a ration of standard white bread at 15% protein on a dry weight basis with varying supplements. When bread was supplemented with 0.5% lysine monohydrochloride, net protein value increased 37% over the control. Altschul (1971) has reported increases of 60% in utilizable protein in wheat flour supplemented with 0.2% lysine.

Lysine requirements for man are 800 milligrams per day (Clark, 1971). For a boy 9-12 years of age, twice as much lysine is required. In developing countries approximately one half of the population is less than 15 years of age (Bennett, 1968). This emphasizes the importance of essential amino acids in the early stages of growth and the problem of adequate diets in developing countries for normal physical and mental development.

Protein quality in human diets may be increased by (1) genetic improvement in economically important plants, (2) greater use of oil-seed meals as direct sources of protein, (3) production and marketing of fish protein concentrates, (4) intensified research to make the production of single cell protein economical and the product palatable, (5) utilization of synthetic amino acids or protein concentrates to increase cereal nutritive value, and (6) extracting leaf proteins (Nelson, 1969). Increasing protein quality by genetic improvement offers the greatest advantage. Through plant breeding, protein quality would be incorporated in a traditional plant food so the adoption of new foods would be unnecessary and the economic, processing, and distribution problems of fortification would be avoided.

Increases by genetic means could be achieved (1) by increasing the ratio of germ to endosperm, (2) by mutations that relieve the genetic limitations regulating the amount of amino acid synthesis, (3) or by genetic control of protein synthesis to change the relative proportions of metabolically inert storage proteins possessing different amino acids (Nelson, 1969).

Mutant recessive genes for high lysine have been reported for corn (Mertz, Bates, and Nelson, 1964), barley (Hagberg, Karlsson, and Munck, 1970), and sorghum (Rameshwar and Axtell, 1973). Mertz, Bates, and Nelson (1964) found the mutant opaque-2 had lysine content (percent of protein) from 3.3% to 4.0%. Normal corn has about 1.3% lysine. Increased lysine content could be attributed to increased lysine in both the zein and acid soluble protein fractions and to a reduction in the ratio of zein to glutelin.

Hagberg, Karlsson, and Munck (1970) reported that a barley of Ethiopian origin had been identified that possessed high protein and high lysine. Inheritance studies indicated the high lysine trait was inherited as a simple recessive factor.

Recent investigations in sorghum by Rameshwar and Axtell (1973) have identified two floury endosperm lines from Ethiopia that produce higher than normal lysine. Lysine (g/100 g protein) was 3.34 and 3.13 at 15.7% and 17.2% protein, respectively. This is a substantial improvement considering normal sorghum lines average 2.05 for lysine and 12.7% for protein.

No simply inherited trait for high lysine such as opaque-2 in corn has been identified in wheat. Major genetic differences for lysine content in wheat could be masked by its hexaploid condition. Johnson, Mattern, and Schmidt (1972b) reevaluated high lysine wheats identified in the World Collection in an array of environments. They concluded the genetic component of variation for lysine to be 0.5%. This genetic component of variation for lysine is relatively small compared to the total variation but it does represent a potential increase of 17% by breeding.

Wheat Kernel Proteins and Kernel Morphology

Wheat proteins can be classified into two categories: endosperm and nonendosperm. The endosperm comprises about 85% of the wheat kernel and contains approximately 70% of the total protein in the grain (Kasarda, Nimmo, and Kohler, 1971). Nonendosperm proteins are higher in lysine than are endosperm proteins, 4% versus 2% (Johnson, Mattern, and Schmidt, 1969a). Milling of the wheat kernel reduces the amount of

nonendosperm protein. Nutritional quality of wheat could be increased by increasing the extraction percent above the conventional 70%.

Endosperm proteins consist of two fractions: (1) gluten and (2) water and salt soluble. Proteins from the gluten portion make up about 85% of the endosperm proteins (Kasarda et al., 1971). Gluten proteins contain gliadins and glutenins which are low in lysine, usually less than 2% (Johnson et al., 1969a). Lysine values of over 4% are representative of the water and salt soluble proteins. Water-soluble proteins generally are highest in low protein wheats, thus resulting in the tendency of higher lysine values found in low protein wheats. Soft texture is typical of wheats possessing high amounts of water-soluble protein.

Morphological characteristics of kernels could change the ratio of endosperm proteins to nonendosperm proteins. This could alter lysine content. Johnson and Mattern (1972c) demonstrated that kernel size of a variety had no effect on either protein or lysine on a dry weight basis. Kernel plumpness and crease characteristics did affect protein content but not lysine as a percentage of protein. They suggested kernel shriveling considerations are warranted for accurate protein and lysine comparisons between wheats.

Protein and Lysine Relationships

Lysine expressed as a unit of protein is inversely related to protein content in wheat. Lawrence et al. (1958) found a highly significant inverse relationship between protein and lysine below 13.5% protein. A highly significant negative correlation ($r = -.68$) between lysine as a percent of protein and protein level was reported by

Villegas, McDonald, and Gilles (1968). Inverse relationships of protein and lysine in wheat flour ranging from 6.7% to 14.0% protein were observed by McDermott and Pace (1960). Vogel, Johnson, and Mattern (1973), in an analysis of 12,613 common wheats in the World Collection, found lysine as a percent of protein to be inversely related up to 15% protein. Protein content of wheats with greater than 15% protein had little effect on lysine content.

Similar inverse relationships have been reported in sorghum (Rameshwar and Axtell, 1973), rice (International Rice Research Institute, 1972), oats (Clark and Potter, 1972), and barley (Munck, 1970). These negative correlations make it difficult to compare lysine content because it varies with protein content. For this reason it has been suggested that lysine values be adjusted to the mean protein level to make comparisons among wheats (Johnson et al., 1968b, Vogel et al., 1973).

Environmental Influences on Protein and Lysine

Protein content of the ripened wheat kernel is determined by climate, soil, and genotype (Leonard and Martin, 1963). Climate and soil conditions do not permit fixed levels of protein to be a breeding goal (Johnson et al., 1973a). However, increased genetic potential for high grain protein can be a breeding goal.

Stroike and Johnson (1972) reported on the stability of protein for varieties grown in the International Winter Wheat Performance Nursery. Three varieties known to possess genes for high protein showed excellent phenotypic expression across environments. The stability of one variety, Atlas 66, was better than the other two varieties.

Johnson, Dreier, and Grabouski (1973b) studied the phenotypic expression of high protein derived from Atlas 66 in a 3-year Nebraska

experiment. Under different levels of nitrogen fertilizer, an experimental line with the Atlas 66 high protein trait maintained an advantage of 2% protein over the check variety Lancer.

Environment also influences the expression of lysine content (Johnson et al., 1972b). In a test of 40 spring wheat varieties grown at three locations in the United States, significant genotype-environment interactions were found by Johnson et al. (1968a). Lawrence et al. (1958) found lysine was not influenced by the year of growth, nor the location except as these affect total protein. They concluded that environment influenced lysine content only as the environment affected the protein level of a wheat.

Breeding for High Protein and High Lysine Content in Wheat

Early studies on wheat protein inheritance were conducted with spring wheat varieties (Clark, 1926; Clark, Florell, and Hooker, 1928; Clark and Quisenberry, 1929). These studies involved parents differing in less than one percent protein. Clark (1926) concluded that protein was inherited as a complex trait; environment greatly influenced protein expression; and protein was often negatively associated with yield. In a review of wheat quality, Hehn and Barmore (1965) stated that it was the experience of Clark and others which discouraged efforts in protein improvement.

Middleton et al. (1954) first reported high grain protein content in Atlas 66. In their study, Atlas 66 produced 3.2 percentage points more protein and was higher yielding than the check variety. Greenhouse studies by Haunold, Johnson, and Schmidt (1962) showed that Atlas 66 produced significantly more grain protein than Comanche and Wichita

5D contribute to high protein. Chromosome substitution of group 5 from Atlas 66 into Chinese Spring supported monosomic evidence that high protein gene(s) are located on chromosome 5D. However, inconclusive evidence by chromosome substitution prevented the establishment of the contribution of 5A and 5B to the expression of high protein.

High protein of Atlas 66 has been transferred to hard red winter wheats. Nebraska experimental lines with Atlas 66 parentage have been as productive or more productive than their parents (Johnson et al., 1969a). One experimental line, NE701132 derived from the cross Atlas 66/Comanche/Lancer, exhibits an advance of 23% in protein and a simultaneous advance of 13% in yield (Johnson, et al., 1972a).

P.I. 176217 (Nap Hal) was identified as a high protein spring wheat by Watson et al. (1966) and Johnson et al. (1971). In an evaluation of a portion of the USDA spring wheat collection, Watson and his group found P.I. 176217 to produce an average protein content of 18.9% over three locations in Montana. Protein performance of Centana and Thatcher check varieties was 16.8% and 17.5%, respectively.

Johnson et al. (1971) reported that in addition to high protein, Nap Hal also possessed high lysine per unit protein. Studies by Johnson et al. (1973a) indicate that Nap Hal consistently produces grain with 0.2 to 0.4% more lysine than Atlas 66 and other varieties with which it has been compared.

Chapman and McNeal (1970) reported on gene effects for grain protein in five spring wheat crosses. One cross involved two high protein parents, P.I. 176217 and Frontiera. By utilizing Hayman's model, they estimated additive and dominance effects. Significant

epistasis was absent in all crosses. Additive effects were significant in all crosses and two crosses including the cross P.I. 176217/Frontiera exhibited significant dominance effects. The apparent dominance was from the Frontiera parent for lower protein.

Transgressive segregation for protein has been observed for both high and low protein in the progeny of Atlas 66 crossed with Nap Hal (Johnson et al., 1973a). Crosses of Nap Hal with two lower-protein wheats, Yung Kwang and Lancer, indicated high protein from Nap Hal to be partially dominant (Johnson and Mattern, 1972).

Kaul and Sosulski (1965) have also observed transgressive segregation for both low and high protein in a Selkirk/Gabo cross. Gabo was two percentage points higher in protein than Selkirk. In this study, broad sense heritability estimates were 82.3% or 79.1%, depending upon the method of calculation. A narrow sense estimate of 66.6% was observed. The authors found no net dominance effects and a bimodal distribution of protein content among F_2 and F_3 plants.

Lebsock et al. (1964) found partial dominance for low protein in the spring wheat cross, P.I. 56219-12/Conley. By regression analysis of F_5 and F_6 means on F_3 lines, heritability estimates of .37 and .70, respectively, were calculated.

April Bearded (C.I. 7337) has been identified as a potential source of high protein and high lysine (Johnson et al., 1969b). In a test of 40 varieties, April Bearded produced significantly more lysine than 37 of the varieties (Johnson et al., 1969b). Tests during 1967-1970 of spring wheats grown in several environments indicated that average yield performance of C.I. 7337 was equal to Justin, average protein

5% higher than Justin, and lysine content 6% higher than Justin (Johnson and Mattern, 1972).

Wheat and wheat related species have been examined for variability in lysine content. Villegas et al. (1968) evaluated lysine in diploid, tetraploid, and hexaploid species. Protein content ranged from 9.9% to 27.0% and lysine ranged from 2.09% to 3.99%. The most outstanding group for lysine content was Triticum boeticum. In their study, rye and triticale were more variable for lysine than spring and durum wheats. Of eight bread wheats studied, Lerma Rojo had the highest average lysine value of 3.02% at an average protein content of 14.12%.

In a study by Lawrence et al. (1958), the highest lysine level was found in wheat-related genera. One hybrid selection from a cross of Agropyron elongatum with wheat had 3.10% lysine. The authors stated that they found certain samples with sufficiently high lysine content to offer hope for breeding improvement.

Qualset et al. (1972) have also suggested that genetic potential exists for improvement of lysine and protein content in wheat. This was based upon positive and significant heritability estimates for both lysine and protein. In their study, 150 wheats selected for high protein and/or lysine were crossed to Inia 66. Both the parents and the hybrids were grown in the field. Heritability was estimated by the correlation of the hybrid with the nonrecurring parent.

MATERIALS AND METHODS

Genetic Materials

Three wheat varieties were selected as parents for this study. Brief descriptions of each parent are given below:

(1) April Bearded, C.I. 7337, is an English spring wheat variety. It has been identified as a source of high protein and high lysine (Johnson et al., 1969a). The spike of April Bearded is awned, long, lax, and glabrous. April Bearded had an average height of 124 cm in this study. Kernels are red in color. Ancestory of April Bearded is unknown. Seed utilized for crossing originated from the source 70GH7221.

(2) Atlas 66, C.I. 12561, is a high protein soft red winter wheat developed from the cross Redhart/Noll/Frondoso. It was released by North Carolina State University in 1949. High protein genes in Atlas 66 probably are from the Frondoso parent, a Brazilian wheat (Johnson et al., 1969b). Lysine content of Atlas 66 averages 0.2% to 0.4% less than Nap Hal at Yuma, Arizona. Spikes of Atlas 66 are awnleted, clavate, and glabrous. Growth habit is intermediate. Its height averaged 115 cm in this study. The parental seed source utilized in this study was 71GH5003.

(3) Nap Hal, P.I. 176217, is an old Indian variety that has been utilized as a source of high protein and high lysine in the AID crossing program at the University of Nebraska.

Spikes of Nap Hal are pubescent, awned, dense, and the tip tends to be laterally compressed. Some parental plants in this study exhibited branched spikes when grown at Yuma, Arizona. This characteristic was also observed in the greenhouse but it was not as pronounced. No branched spikes were observed in the nursery at Fort Collins, Colorado. Spike color was bronze under environmental conditions at Yuma, Arizona, and white under greenhouse conditions in Lincoln, Nebraska. Kernels are red and soft textured. Nap Hal has spring growth habit and early maturity. Of the three parents Nap Hal is the shortest; its height in this study averaged 95 cm. The seed source used for crossing was 70GH3529.

Parental seed sources originated from selfed individual plants grown in the greenhouse. The parents were crossed in diallel fashion without reciprocals. For each of the three single crosses, backcrosses and F_2 populations were developed in the greenhouse. A total of 15 populations were developed as shown in Table 1. For purpose of discussion, the abbreviations AB, ATL, and NP will be utilized for April Bearded, Atlas 66, and Nap Hal, respectively.

Locations

Two irrigated locations, Yuma, Arizona, and Fort Collins, Colorado, were selected for this investigation. Yuma, Arizona, represents a highly productive environment located at 32° 40' N latitude and 114° 40' W longitude. Vernalization requirements for winter wheats are satisfied so both spring and winter wheats can be grown from fall

Table 1. Populations, generations, abbreviations, and the number of rows per replication utilized in this study.

Population	Generation[1/]	Abbreviation	Number of rows per rep
April Bearded	P	AB	1
Atlas 66	P	ATL	1
Nap Hal	P	NP	1
April Bearded/Atlas 66	F_1	AB/ATL F_1	1
April Bearded/Nap Hal	F_1	AB/NP F_1	1
Atlas 66/Nap Hal	F_1	ATL/NP F_1	1
2*April Bearded/Atlas 66	BC	2*AB/ATL	1
April Bearded/2*Atlas 66	BC	AB/2*ATL	1
2*April Bearded/Nap Hal	BC	2*AB/NP	1
April Bearded/2*Nap Hal	BC	AB/2*NP	1
2*Atlas 66/Nap Hal	BC	2*ATL/NP	1
Atlas 66/2*Nap Hal	BC	ATL/2*NP	1
April Bearded/Atlas 66	F_2	AB/ATL F_2	2
April Bearded/Nap Hal	F_2	AB/NP F_2	2
Atlas 66/Nap Hal	F_2	ATL/NP F_2	2

1/ P, F_1, F_2, and BC represent parent, first filial, second filial, and backcross generations, respectively.

planting. Planting date of the nursery at Yuma was December 3, 1972. Harvest dates were May 25-29, 1973.

Fort Collins, Colorado, is a high altitude location (1525 m) at 40° 46' N latitude and 105° 04' W longitude. Environmental conditions at Fort Collins are conducive to maximum grain production. Spring rains delayed planting until April 12, 1973. Cool temperatures after planting were satisfactory for the vernalization requirement of Atlas 66. Plants were harvested August 22-23, 1973.

Both locations were irrigated to minimize soil moisture stress. Soil fertility was adequate at each location. Before planting at Yuma, 100 pounds of nitrogen was applied per acre. The Fort Collins nursery was planted on land that had previously been planted to beans.

Weeds were controlled throughout the growing season. Timely hoeing controlled weeds at Yuma. At Fort Collins, one application of 2,4-D was applied before the boot stage of growth. Later, weeds were controlled by hoeing.

Diseases were not a problem at Yuma. A late infection of stem rust (*Puccinia graminis tritici*) and leaf rust (*Puccinia recondita*) developed at Fort Collins at the end of July. The nursery was sprayed twice with Manzate-D fungicide to control additional infection and loss. Disease infection occurred at the milky to soft dough stage of kernel development.

Bird damage occurred at Yuma on a few plants. Generally, insect or bird damage was insignificant at both locations.

Experimental Design and Procedure

Fifteen populations were grown in a randomized complete block design with four replications at two locations. A single plot of one row was sown for each P, F_1, and BC generation in each replication. Two plots per replication were sown of each F_2 generation (Table 1).

Each plot consisted of one 3.75 m row with seeds spaced 15 cm apart. Rows were spaced 60 cm apart to minimize interplot competition. Two seeds of Lerma Rojo were planted at the ends of each row to reduce competition effects. The outside rows of each replication also were sown with Lerma Rojo seeds spaced 15 cm apart.

At Yuma, the nursery was planted by hand whereas the nursery at Fort Collins was planted with the aid of a jab-type hand planter. Some double plantings occurred at Fort Collins and one plant of each double had to be removed. Approximately 70% of the seeds planted at Yuma germinated. At Fort Collins germination was near 100% with the primary loss of plants attributed to double plantings.

A problem was encountered in producing backcross seed of the genotype ATL/2*NP. Few crossed seeds were made in time for the Yuma planting because niching was poor. The ATL/NP F_1 was late maturing in the greenhouse while Nap Hal was early. In addition, Nap Hal is a poor pollen shedder. At Yuma, seed stocks of this genotype were divided among the four replications and Lerma Rojo seeds were added to complete the row. Planting at Fort Collins was later which made it possible to make additional crosses to replenish seed supplies.

Plants were harvested in the field with a plant thresher. In addition to experimental plants, sixteen Lerma Rojo plants were threshed to sample a variety with lower protein content that was grown under the

same environmental conditions. Two competitive Lerma Rojo plants were harvested from each end of the four replications.

Traits Measured

Protein and lysine content was determined for individual plants that yielded 5 grams or more. Whole kernel samples were ground using a Udy Cyclone Sample Mill. Samples were then placed in a controlled humidity cabinet to achieve a constant moisture level. Flour samples were weighed on a dry matter basis. Duplicate samples for each plant were analyzed for protein by the Kjeldahl procedure. Control samples were included at 24-sample intervals. Protein values were calculated as percent nitrogen multiplied by 5.7. Samples with extremely shriveled kernels (shrivel index greater than 36) were excluded from statistical analysis.

Lysine determinations were made by the ion-exchange chromatography method. Samples were acid hydrolyzed and then analyzed with an automatic amino acid analyzer modified with four short columns. This procedure is programmed so that only the lysine peak is recorded and integrated.

Suspect determinations of samples were repeated where seed supplies permitted.

Data were recorded for the following characteristics of each harvested plant:

Plant height -- Height measured in centimeters from ground level to the tip of the tallest spike of each plant excluding the awns.

Plant yield -- Grain yield of each plant measured to the nearest whole gram.

Kernel weight -- Weight in milligrams determined by weighing 100 kernels from each plant and dividing by 100.

Kernel size -- Visual measurement of kernel size based on the scale 1-5; 1 indicates extremely small kernels, 3 indicates medium size, and 5 represents large kernels.

Shriveling type -- Visual measurement of the degree of kernel shriveling based on the scale 1-5; 1 indicates plump kernels, 3 indicates crease open, cheeks not rounded, and 5 indicates extreme shriveling.

Shriveling frequency -- Visual measurement of the percent of kernels showing a given shrivel type based on the scale 0-9.

Shriveling index -- Shriveling type multiplied by shriveling frequency; scale 0-45.

Competition factor -- Individual plants scored on a scale of 1-3; 1 if the plant was not bordered by adjacent plants in the row, 2 if the plant was bordered by one adjacent plant, and 3 if the plant competed with both adjacent plants.

Statistical Analyses

Means, variances, ranges, and coefficients of variation were computed for each population by pooling individual plant data from the four replications. In addition, correlations were computed on individual plant data within populations and among all populations.

To obtain an estimate of within-plant variation for each population, a nested analysis of variance was utilized. Plants were considered nested in replications for parent, F_1, and backcross populations. In F_2 populations, plants were nested in plots and replications.

Analysis of variance for a randomized complete block design of generation means from each replication was utilized for all measured traits. Mean comparisons were made using the LSD when the computed F value was significant for treatment differences in the analysis of variance.

All statistical analyses were computed with the aid of an IBM 360 computer. Statistical Analysis System (SAS) was implemented for statistical processing (Service, J., 1972). Statistical procedures and interpretation were followed as outlined by Snedecor and Cox (1967), Cochran and Cox (1957), Sokol and Rohlf (1969), and LeClerg, Leonard, and Clark (1962).

Genetic Analyses

To study hereditary and environmental influences quantitive genetic analyses were utilized. Phenotypic variability of a trait is due to variations from genetic, environmental, and genetic by environmental interaction sources. Genetic variance was first separated into three components by R. A. Fisher (1918). The three components Fisher used were: additive effects of genes, dominance deviations from the additive scheme, and deviations from the additive scheme attributable to interallelic interactions. Mather and Jinks (1971) and Hayman (1958) have estimated gene effects as linear functions of the means of six populations: P_1, P_2, F_1, F_2, BC_1, and BC_2. From these means six parameters can be

estimated: mean effects, additive gene effects, dominance gene effects, and the three types of digenic epistatic effects. Hayman (1958) symbolized these estimates of gene action by m, d, h, i, j, and l to represent mean, additive, dominance, additive by additive, additive by dominance, and dominance by dominance effects, respectively. Gamble (1962) utilized the corresponding symbols m, a, d, aa, ad, and dd which are more meaningful to plant breeders.

In this study, Hayman's model (1958) for determining the expression of gene effects based on generation means was utilized. A computer program written by Lee and Kaltsikes (1971) for weighted (by the inverse of the variance for the generation means) least squares analysis of Hayman's model was implemented. First the three parameter model for m, a, and d is fitted. The deviations of expected from observed are tested by chi-square. A significant chi-square indicates nonfit and the possibility of epistasis. The six parameter model should then be employed to test for epistasis. Failure to fit the six parameter model may indicate trigenic epistasis or linkage or both.

Warner (1952) described a method to estimate heritability based on the model described by Mather. Warner's method estimates heritability on the basis of the F_2 and the backcross of the F_1 to each inbred parent. An estimate of the nonheritable variance is unnecessary. It is assumed the environmental components in the three segregating populations (BC_1, BC_2 and F_2) are comparable. The formula for computing Warner's heritability is: $H = \frac{2V_{F2} - (V_{BC1} + V_{BC2})}{V_{F2}}$, where V_{F2}, V_{BC1}, and V_{BC2} are the total variances within the F_2 generation and the two backcrosses to the respective parents.

Heritability can also be estimated approximating the nonheritable variance from genetically uniform populations, that is nonsegregating populations. Burton (1952) used the formula, $H = \frac{V_{F2} - V_{F1}}{V_{F2}}$, where V_{F2} equals the variance of the F_2 population and V_{F1} is the variance of the F_1 population. Petr and Frey (1966) used the formula, $H = \frac{V_{F2} - (V_{P1} \times V_{P2})^{\frac{1}{2}}}{V_{F2}}$. In this case V_{F2} is the variance of the F_2 and V_{P1} and V_{P2} are the variances of the respective parents. These are broad sense heritability estimates and the numerator includes all of the nonadditive as well as the additive genetic variance.

EXPERIMENTAL RESULTS

Frequency distributions for protein and lysine in F_2 populations indicated that the distributions were not bimodal. Population distributions of the F_2 generations were then checked for normality by plotting the cumulative normal curve on normal probability paper. If the cumulative normal curve approximates a straight line, then the distribution is approximately normal. Only small departures from a straight line were obtained which indicated that these populations were approximately normal.

Means, variances, ranges, and coefficients of variation for all traits measured are given in the appendix (Tables A1-11). These statistics are based on individual plant data grouped across replications and plots to form one sample. Genotypic means in each of four replications at a location were analyzed as a randomized complete block. The analyses of variance indicated that genotypes were a significant source of variation for all measured traits (Table A12). Means and LSD's from analyses of Yuma and Fort Collins data are given in Tables 2 and 3, respectively.

Table 4 lists means, standard deviations and coefficients of variation for sixteen Lerma Rojo plants at each location. Direct comparisons between Lerma Rojo and other genotypes are not strictly valid because Lerma Rojo was not included in the experimental design.

Primary emphasis will be given to protein and lysine performance of these genotypes. Other measured traits will be discussed as they relate to protein and lysine.

Protein

At Yuma, Nap Hal produced grain with about one percentage point more

Table 2. Means and LSD's of measured traits for 15 genotypic means in four replications at Yuma, Arizona in 1973.

Genotype	Protein %	Lysine % protein	Adj lys %	Lys % dry wt	Plant yield gms	Kernel weight mg	Plant ht cm	Kernel size 1-5	Shriv type 1-5	Shriv freq 0-9	Shriv index 0-45
Parents:											
April Bearded	19.12	2.91	3.11	.551	30.75	33.54	139.2	3.3	2.7	2.7	7.8
Atlas 66	19.35	2.75	2.96	.528	36.58	35.47	128.2	3.5	2.9	4.7	14.0
Nap Hal	20.44	3.06	3.26	.619	23.31	22.34	112.8	2.6	2.6	3.4	9.9
F_1's:											
April Bearded/Atlas 66	18.68	2.88	3.08	.532	36.40	36.19	144.4	3.3	2.8	4.3	12.6
April Bearded/Nap Hal	19.39	2.94	3.15	.565	38.59	30.62	142.3	3.2	2.4	2.6	6.9
Atlas 66/Nap Hal	18.31	2.94	3.14	.532	38.86	33.44	135.8	3.5	2.7	2.8	8.1
BC's:											
2*April Bearded/Atlas 66	18.02	2.96	3.15	.525	30.26	35.96	147.1	3.4	2.7	2.7	7.7
April Bearded/2*Atlas 66	18.96	2.82	3.02	.528	33.79	36.26	143.3	3.4	2.7	3.7	10.6
2*April Bearded/Nap Hal	19.66	2.92	3.13	.569	34.71	31.64	140.4	3.1	2.7	3.5	10.1
April Bearded/2*Nap Hal	19.76	3.01	3.21	.590	29.59	27.72	126.9	3.1	2.6	3.1	9.1
2*Atlas 66/Nap Hal	18.86	2.83	3.03	.529	36.83	34.36	129.2	3.3	2.8	3.6	11.0
Atlas 66/2*Nap Hal	17.89	3.00	3.20	.532	39.49	30.11	130.2	3.1	2.5	2.3	6.5
F_2's:											
April Bearded/Atlas 66	18.80	2.89	3.09	.537	38.81	36.34	147.7	3.3	2.7	2.9	8.5
April Bearded/Nap Hal	19.84	3.00	3.20	.589	31.32	27.98	135.9	3.0	2.6	2.9	8.7
Atlas 66/Nap Hal	19.46	2.87	3.07	.553	35.76	29.70	128.6	3.1	2.9	3.9	12.1
Grand Mean	19.10	2.92	3.12	.552	34.34	32.11	135.5	3.2	2.7	3.3	9.6
LSD .05	1.00	.08	.08	.024	7.72	2.24	7.1	.2	.3	1.2	4.0
LSD .01	1.34	.11	.10	.033	10.32	2.99	9.5	.3	.4	1.7	5.4

Table 3. Means and LSD's of measured traits for 15 genotypic means in four replications at Fort Collins, Colorado in 1973.

Genotype	Protein %	Lysine % protein	Adj lys %	Lys % dry wt	Plant yield gms	Kernel weight mg	Plant ht cm	Kernel size 1-5	Shriv type 1-5	Shriv freq 0-9	Shriv index 0-45
Parents:											
April Bearded	16.67	2.99	3.18	.493	18.20	25.64	106.3	3.0	3.3	5.5	18.5
Atlas 66	21.34	2.60	2.80	.551	19.78	28.11	100.7	3.3	3.2	5.9	19.3
Nap Hal	17.19	3.05	3.26	.519	16.57	20.73	76.5	3.0	3.1	4.1	12.9
F_1's:											
April Bearded/Atlas 66	18.10	2.76	2.97	.494	27.79	33.77	112.1	3.8	3.0	3.7	11.2
April Bearded/Nap Hal	15.77	3.05	3.23	.477	20.20	25.44	97.0	3.1	3.1	4.0	12.6
Atlas 66/Nap Hal	17.39	2.87	3.08	.495	24.49	28.58	95.6	3.2	3.0	3.9	11.9
BC's:											
2*April Bearded/Atlas 66	18.12	2.84	3.04	.509	19.44	29.01	109.7	3.2	3.2	5.1	16.8
April Bearded/2*Atlas 66	19.59	2.69	2.90	.522	22.95	30.67	105.4	3.4	3.2	4.4	14.1
2*April Bearded/Nap Hal	16.54	3.04	3.23	.498	16.49	24.81	102.4	3.0	3.2	5.4	17.8
April Bearded/2*Nap Hal	16.86	3.11	3.31	.519	15.85	20.91	85.3	3.0	3.4	6.2	21.9
2*Atlas 66/Nap Hal	19.63	2.75	2.96	.536	19.41	26.91	100.8	3.2	3.3	5.1	17.3
Atlas 66/2*Nap Hal	17.50	2.96	3.16	.512	19.17	23.82	82.9	3.1	3.2	4.3	14.1
F_2's:											
April Bearded/Atlas 66	18.56	2.79	3.00	.512	23.20	29.73	107.5	3.3	3.0	4.7	14.7
April Bearded/Nap Hal	16.57	3.04	3.23	.498	16.86	23.83	94.7	3.2	3.0	5.7	17.3
Atlas 66/Nap Hal	18.94	2.87	3.07	.537	17.40	25.21	90.8	3.1	3.2	5.7	18.4
Grand Mean	17.92	2.89	3.09	.511	19.85	26.48	97.8	3.2	3.2	4.9	15.9
LSD .05	.80	.08	.08	.022	2.74	1.33	4.7	.2	.2	1.1	3.9
LSD .01	1.07	.10	.10	.029	3.67	1.78	6.3	.2	.2	1.4	5.2

Table 4. Means, standard deviations, and coefficients of variation of measured traits for sixteen Lerma Rojo border plants grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Trait	Yuma			Fort Collins		
	$\bar{X}$	SD	CV %	$\bar{X}$	SD	CV %
Protein	15.88	.83	5.2	19.14	1.25	6.5
Lysine (% protein)	2.80	.09	3.2	2.60	.08	3.1
Adjusted lysine %	2.99	.06	2.0	2.81	.08	2.9
Lysine % (dry wt)	.44	.05	1.1	.49	.03	5.0
Plant yield (gms)	53.70	22.57	42.8	18.5	3.44	18.6
Kernel weight (mg)	46.80	4.46	9.5	38.9	2.67	6.9
Kernel size (1-5)	4.80	.45	9.4	4.0	0.0	0.0
Shrivel type (1-5)	2.80	.40	14.3	3.0	0.0	0.0
Shrivel frequency (0-9)	1.30	.70	53.9	2.2	1.1	50.4
Shrivel index (0-45)	3.80	2.24	59.0	6.6	3.32	50.6

protein than April Bearded and Atlas 66 (Table 2). Protein contents of April Bearded and Atlas 66 did not differ significantly. At Fort Collins, Atlas 66 had approximately four percentage points more protein than April Bearded and Nap Hal (Table 3). Protein expression of April Bearded and Nap Hal was not statistically different at this location.

At Yuma, the F_1 and F_2 generation means of April Bearded/Atlas 66 were lower than the parental means. The same F_1 and F_2 generation means at Fort Collins fell between the parental means and were closer to the low protein parent April Bearded. F_1 and F_2 means of this cross were not statistically different at either location.

The F_1 and F_2 means of the April Bearded/Nap Hal cross were between the parent protein levels at Yuma. The F_1 was nearer the low protein parent, April Bearded, while the F_2 mean approached the mid-parent value of 19.78%. At Fort Collins, the F_1 and F_2 of this cross had lower protein content than either parent. Means of the F_1 and F_2 generations were not statistically different.

F_1 performance of the Atlas 66/Nap Hal cross at Yuma was 1.04% lower than the low protein parent Atlas 66. The F_2 mean of this cross approached the protein content of Atlas 66. At Fort Collins, the F_1 mean for this cross approximated the low protein parent Nap Hal. The F_2 mean approached the mid-parent value of 19.27%. Differences of F_1 and F_2 means were significant for this cross.

Only the backcrosses of the Atlas 66/Nap Hal cross differed significantly at Yuma. The Atlas 66/2*Nap Hal backcross failed to produce mean protein levels approaching the Nap Hal parent. The mean of this backcross may be subject to sampling error because seed stocks of the population limited the number of backcross plants in the experiment. At

Fort Collins, backcross populations differed significantly in April Bearded/Atlas 66 and Atlas 66/Nap Hal crosses but not in the April Bearded/Nap Hal cross.

Lysine

Lysine in this study has been reported as percent of protein, adjusted lysine percent, and lysine percent on a dry grain weight basis (or lysine percent of sample). Adjusted lysine percent is based upon the third degree polynomial model utilized by Vogel et al. (1973) to describe the curvilinear relationship between protein and lysine (% of protein) of common wheats in the USDA World Collection. Lysine percent of protein values are adjusted to a mean protein level of 12.97%. In this study adjusted values are a consistent addition of about 0.2% lysine to unadjusted lysine values expressed as a percent of protein. This is in agreement with the negative relationship Vogel et al. (1973) found between lysine percent of protein and protein up to 15% protein. Protein had little influence on lysine content of protein for wheats above 15% protein. Average protein contents in this study were above 15%. Lysine percent on a dry grain weight basis is highly correlated with protein content. The best measure of protein quality is lysine expressed as a percent of protein. Further comparisons and discussion of lysine will be confined to lysine as percent protein where values are not adjusted.

Nap Hal had the highest lysine content (percent of protein) of the parents at both locations (Tables 2 and 3). At Yuma, Nap Hal had significantly more lysine than either April Bearded or Atlas 66. Lysine level of Nap Hal was significantly higher than Atlas 66 only at Fort Collins. April Bearded produced significantly more lysine than

Atlas 66 at both locations.

Figures 1 and 2 show the linear relationship between lysine as a percent of protein and protein for the parents grown at Yuma and Fort Collins, respectively. Lerma Rojo is also included based upon the limited data from border-row plants. The simple linear regression models do not explain a large percent of the variation between lysine and protein. However, the models do indicate the probably lysine level of the parents at different protein levels.

The lysine values of all F_1 generations were between parental lysine values of the cross and often near mid-parent values. Performance of the F_2 generations was not significantly different from the F_1 performance. Backcross performance tended to approach the recurrent parent. Backcross generations within a cross differed significantly at the 5% level with only one exception (Tables 2 and 3). At Fort Collins, the 2*April Bearded/Nap Hal mean did not differ from the April Bearded/2*Nap Hal mean for lysine content.

Population Variances

Between plant variances within populations are given in Table 5. These variances were determined by a nested analysis of variance for each population (Tables A13-14). Variances for protein in nonsegregating populations were large in comparison to segregating population variances at Yuma (Table 5). At Fort Collins, protein variances were greater for April Bearded and Atlas 66 than for other nonsegregating populations.

Variances of the F_1 populations were used to test for statistically significant increases of protein and lysine variances in the F_2 populations (Table 6). Since several parental variances were not homogenous, pooled variances of the parents were not used to test F_2 variances.

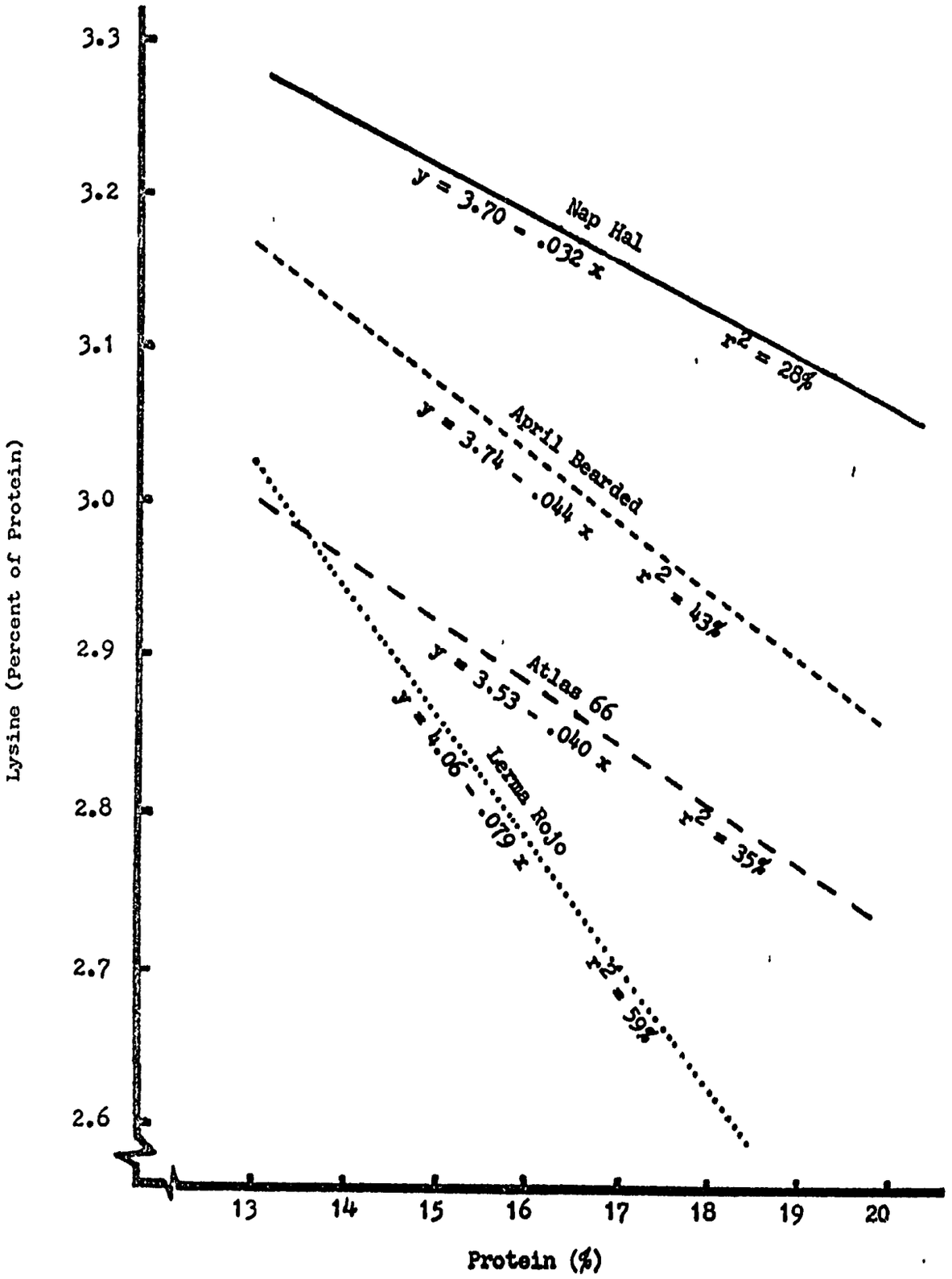

Figure 1. Linear relationship of lysine as a percent of protein with protein for April Bearded, Atlas 66, Nap Hal and Lerma Rojo grown at Yuma, Arizona in 1973.

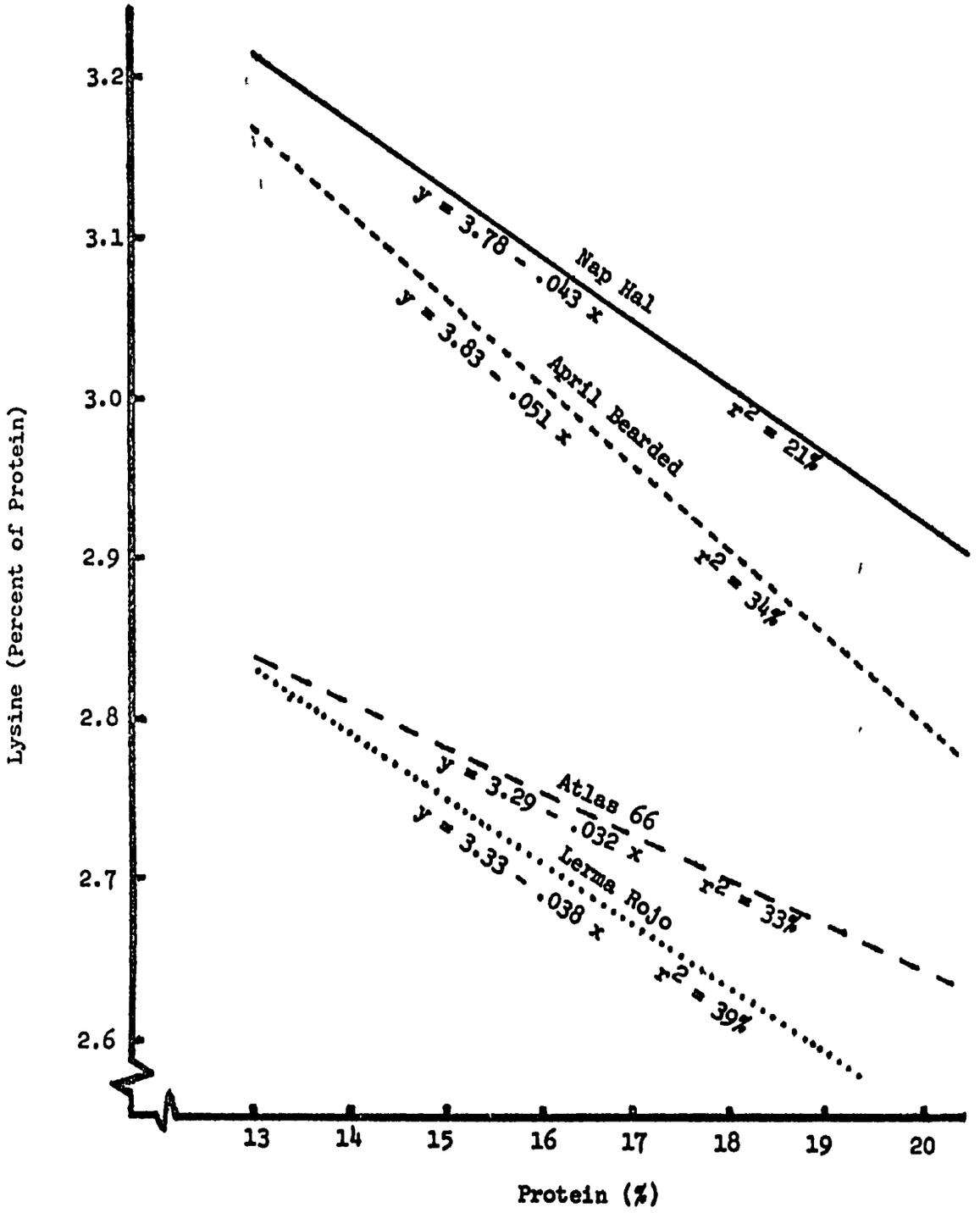

Figure 2. Linear relationship of lysine as a percent of protein with protein for April Bearded, Atlas 66, Nap Hal and Lerma Rojo grown at Fort Collins, Colorado in 1973.

Table 5. Between plant variances within populations for protein percent and lysine as a percent of protein in 15 genotypic populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Genotype	Protein		Lysine	
	Yuma	Fort Collins	Yuma	Fort Collins
Parents:				
AB	2.4724	3.0339	.0091	.0190
ATL	1.1169	2.9480	.0072	.0084
NP	2.5914	.5859	.0069	.0046
F_1's:				
AB/ATL	2.5246	1.1448	.0124	.0100
AB/NP	1.6585	.9834	.0099	.0140
ATL/NP	3.4009	1.2913	.0116	.0090
BC's:				
2*AB/ATL	3.9308	4.0809	.0173	.0181
AB/2*ATL	2.1010	3.9344	.0175	.0121
2*AB/NP	2.6680	2.4222	.0132	.0168
AB/2*NP	3.8551	1.3209	.0120	.0109
2*ATL/NP	3.5751	3.6387	.0088	.0125
ATL/2*NP	3.2170	2.4779	.0191	.0130
F_2's:				
AB/ATL	2.3341	4.3150	.0124	.0232
AB/NP	3.6092	2.7735	.0167	.0181
ATL/NP	3.1560	5.1317	.0126	.0215

Table 6. F values to test for equal variances of protein and lysine between F_1 and F_2 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Population	Yuma			Fort Collins		
	df	Variance	F	df	Variance	F
AB/ATL						
Protein						
F_2	142	2.3341	.92	175	4.3150	3.77**
F_1	67	2.5246		87	1.1448	
Lysine						
F_2	142	.0124	1.00	175	.0232	2.32**
F_1	67	.0124		87	.0100	
AB/NP						
Protein						
F_2	139	3.6092	2.18**	176	2.7735	2.82**
F_1	68	1.6585		95	.9834	
Lysine						
F_2	139	.0167	1.69**	176	.0181	1.29
F_1	68	.0099		95	.0140	
ATL/NP						
Protein						
F_2	143	3.1560	.93	173	5.1317	3.94**
F_1	73	3.4009		86	1.2913	
Lysine						
F_2	143	.0126	1.09	173	.0215	2.39**
F_1	73	.0116		86	.0090	

*Indicates significance at the 5% level.
**Indicates significance at the 1% level.

The April Bearded/Nap Hal population was the only population at Yuma in which F_2 variances for protein and lysine were different from F_1 variances. At Fort Collins, all F_2 variances were significantly greater than their respective F_1 variances except for lysine in April Bearded/Nap Hal.

Genotype-Environment Interaction

The combined analyses of variance for protein and lysine are given in Table 7. Replication, location, and genotypes are assumed to be fixed effects in these analyses. The genotype-location interaction was highly significant for both protein and lysine. Mean protein content of the parents and other genotypes was not consistent from location to location (Tables 2 and 3). The rank of lysine content for parents was similar across locations but the F_1 and segregating populations changed in performance by rank.

Correlated Responses

Protein. Table 8 reports the phenotypic correlations between protein and other traits measured on individual plants for each population. Protein content was negatively related to lysine as a percent of protein and to adjusted lysine. High significant positive correlations existed between protein and lysine expressed as a percent dry weight.

Yield per plant and protein content were generally inversely related within populations and among all individual plants. Most of these inverse correlations were less than -.50. This indicates that less than 25% of the variation in protein could be explained by yield.

Correlations between protein content and kernel weight were in general negative within populations. The magnitude of these correlations varied widely but they tended to be higher in nonsegregating populations.

Table 7. Combined analyses of variance (fixed model) over locations for protein and lysine as a percent protein.

		Protein			Lysine		
Source	df	Mean square	F	P	Mean square	F	P
Location	1	41.9492			.022141		
Reps/Location	6	3.3726			.030679		
Genotype	14	4.5261	11.37	.0001	.102444	34.42	.0001
Genotype x Location	14	6.2702	15.76	.0001	.016903	5.68	.0001
Error	84	.3979			.002977		
Total	119	2.0736			.017875		

Table 8. Phenotypic correlations between protein and other traits measured on individual plants of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

			Protein vs.										
Population	Loc	n	Lysine % protein	Adj. lys %	Lys % dry wt	Plant yield	Kernel weight	Plant ht	Kernel size	Shrivel type	Shrivel freq.	Shrivel index	Comp. factor
Parents:													
AB	Y	69	-.65**	-.68**	.91**	-.29*	-.52**	-.05	-.20	.43**	.53**	.56**	.06
	FC	92	-.58**	-.54**	.86**	-.44**	-.24*	-.28**	-.12	.35**	.23*	.32**	.23*
ATL	Y	63	-.59**	-.61**	.88**	-.13	-.17	-.11	-.08	.34**	.60**	.61**	-.32**
	FC	97	-.58**	-.63	.90**	-.54**	-.77**	-.22*	-.49**	.47**	.58**	.66**	.01
NP	Y	63	-.53**	-.58**	.92**	-.52**	-.63**	.11	-.41**	.68**	.65**	.69**	.23
	FC	93	-.46**	-.42**	.86**	-.37**	-.17	-.15	-.05	.26**	.28**	.33**	-.01
F_1's:													
AB/ATL	Y	71	-.73**	-.69**	.89**	-.19	-.40**	-.07	-.07	.31**	.52**	.54**	.20
	FC	91	-.50**	-.60**	.75**	.02	-.35**	-.01	-.47**	.20*	.38**	.39**	-.23*
AB/NP	Y	72	-.31**	-.39**	.88**	-.41**	-.55**	-.28*	-.13	.44**	.63**	.65**	.13
	FC	99	-.29**	-.16	.74**	-.26**	-.27**	-.53**	-.04	.19*	.43**	.44**	-.20*
ATL/NP	Y	77	-.70**	-.64**	.93**	-.22	.06	.02	-.01	.50**	.39**	.45**	.10
	FC	90	-.37**	-.36**	.79**	-.32**	-.50**	-.29**	-.11	.56**	.43**	.54**	-.15
BC's:													
2*AB/ATL	Y	70	-.84**	-.77**	.94**	-.02	-.14	-.32**	-.11	.48**	.51**	.54**	-.08
	FC	93	-.49**	-.47**	.89**	-.28**	-.04	-.15	-.12	.12	.12	.14	-.03
AB/2*ATL	Y	79	-.68**	-.69**	.74**	-.23*	.09	-.23*	.24*	.25*	.39**	.34**	-.20
	FC	95	-.63**	-.67**	.91**	-.42**	-.18	-.14	-.03	.25**	.25**	.28**	-.04
2*AB/NP	Y	75	-.53**	-.57**	.85**	-.23*	-.26*	-.08	.01	.45**	.49**	.52**	.03
	FC	89	-.33**	-.20	.89**	-.48**	-.21*	-.09	-.18	-.21*	.44**	.45**	.00
AB/2*NP	Y	67	-.52**	-.57**	.91**	-.54**	-.29*	-.22	-.18	.30**	.47**	.49**	-.03
	FC	81	-.30**	-.23*	.85**	-.40**	-.42**	-.38**	-.44**	.46**	.37**	.46**	.00
2*ATL/NP	Y	73	-.50**	-.40**	.94**	-.10	-.12	-.12	-.11	.50**	.50**	.57**	-.04
	FC	93	-.55**	-.60**	.91**	.49**	-.43**	.09	-.31**	.38**	.49**	.53**	-.05
ATL/2*NP	Y	26	-.63**	-.57**	.89**	-.13	-.32	.09	-.15	.18	.47**	.48**	-.07
	FC	86	-.71**	-.70**	.87**	-.20	.14	-.21*	.17	.08	.07	.07	.02

Table 8. (Continued)

Population	Loc	n	Protein vs. Lysine % protein	Adj. lys %	Lys % dry wt	Plant yield	Kernel weight	Plant ht	Kernel size	Shrivel type	Shrivel freq.	Shrivel index	Comp. factor
F_2's:													
AB/ATL	Y	150	-.61**	-.60**	.89**	-.16*	-.15	-.11	.07	.41**	.47**	.47**	-.01
	FC	183	-.68**	-.69**	.87**	-.16*	.13	-.16*	-.05	.03	.01	.01	-.12
AB/NP	Y	147	-.48**	-.54**	.90**	-.34**	-.32**	-.25**	-.21**	.36**	.36**	.52**	.05
	FC	184	-.64**	-.56**	.90**	-.30**	-.08	.02	.02	.25**	.22**	.27**	-.16*
ATL/NP	Y	151	-.58**	-.61**	.89**	-.37**	-.23**	-.17*	-.17*	.40**	.44**	.48**	.09
	FC	181	-.47**	-.50**	.88**	-.42**	.00	.03	.01	.19**	.13	.16*	-.11
Among all individual plants	Y	1253	-.43**	-.43**	.87**	-.28**	-.36**	-.21**	-.19**	.36**	.47**	.49**	.03
	FC	1647	-.70**	-.70**	.84**	-.14**	.13**	.06*	.07**	.21**	.20**	.24**	-.05

*Indicates significance at the 5% level.
**Indicates significance at the 1% level.

Correlations between plant height and protein were significant at the 5% level in five nonsegregating populations. Correlations of protein and plant height among all individual plants were -.21 at Yuma and .06 at Fort Collins. The negative correlation of -.21 probably reflects greater effect of environment at Yuma. At Fort Collins, populations were more uniform in height and the magnitude of the correlation coefficient among all individual plants was smaller.

Correlations between protein and kernel size varied in magnitude and sign. Significant negative correlations were obtained in three nonsegregating populations. These negative values indicate that as seed size increased protein decreased. There were no consistent correlations of a genotype across locations.

In most populations, as the shrivel type or degree of shriveling increased, protein also increased. Many of these correlations had similar magnitudes and were present in nonsegregating populations as well as segregating populations.

Shriveling frequency was significantly correlated with protein in 26 of 30 populations. All correlations were positive which reflects association of higher protein with increased shriveling.

Shrivel index also was highly associated with protein content. With few exceptions the magnitude of these correlations was little different in nonsegregating populations and segregating populations.

Competition factor was included in the correlations in an effort to assess the influence of adjacent plant competition on protein content. No consistent relationship could be established. The influence of competition, as measured in this study, generally had little influence on protein.

Lysine. Phenotypic correlations between lysine as a percent of protein and other traits measured on individual plants are given in Table 9. Lysine as a percent of protein was highly correlated with adjusted lysine percent of protein. No consistent relationships were detected between lysine (percent of protein) and lysine (percent of dry weight).

Three significant positive correlations between lysine percent of protein and plant yield were detected. The magnitude of these correlations was small.

Lysine as a percent of protein was correlated with kernel weight in several populations but these were not consistent in sign. Among all individual plants, negative correlations of -.15 and -.52 were determined at Yuma and Fort Collins, respectively. The larger correlation coefficient at Fort Collins probably was due largely to smaller seed size and to a greater amount of shriveling.

Correlation of plant height with lysine percent was not consistent. Among all individual plants, negative correlations existed between lysine and plant height at each location.

Kernel size and lysine content exhibited no consistent relationship within populations. In general, kernel size was negatively related to lysine percent among all individual plants.

Generally, lysine percent of protein was not consistently related to shrivel type, shrivel frequency, or shrivel index. At Yuma, a negative correlation among all individual plants was found, while at Fort Collins, a positive correlation between lysine and these traits existed. Higher lysine content in Atlas 66 was associated with less shriveling.

Table 9. Phenotypic correlations between lysine as a percent protein and other traits measured on individual plants of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

			Lysine (% protein) vs.									
Population	Loc	n	Adj. lys %	Lys % dry wt	Plant yield	Kernel weight	Plant ht	Kernel size	Shrivel type	Shrivel freq	Shrivel index	Comp. factor
Parents:												
AB	Y	69	.99**	-.28*	.06	.27*	-.19	.25*	-.20	-.20	-.21	-.17
	FC	92	.99**	-.10	-.09	-.41**	-.05	-.01	.16	.19	.22*	.17
ATL	Y	63	.99**	-.16	-.04	.25*	-.05	.08	-.10	-.45**	-.44**	.13
	FC	97	.99**	-.17	.20*	.27**	-.20*	.14	.00	-.34**	-.28**	-.04
NP	Y	63	.99**	-.15	.15	.31**	-.22	.20	-.33**	-.21	-.21	-.22
	FC	93	1.00**	.05	-.05	-.28	.11	-.03	-.04	-.02	-.04	.18
F_1's:												
AB/ATL	Y	71	.99**	-.35**	.12	.40**	-.06	.15	-.29**	-.29**	-.32**	-.26*
	FC	91	1.00**	.08	-.03	-.07	-.21	.23*	-.09	-.38**	-.38**	.12
AB/NP	Y	72	.99**	.16	.08	.22	-.05	.02	-.25*	-.23*	-.25*	.00
	FC	99	.99**	.41**	-.15	-.28**	-.03	-.12	.13	-.13	-.06	.06
ATL/NP	Y	77	.98**	-.39**	.18	.13	-.18	.18	-.20	-.31**	-.32**	.03
	FC	90	1.00**	.27**	.11	.22*	.31**	.05	-.08	-.12	-.15	.00
BC's:												
2*AB/ATL	Y	70	.97**	-.61**	-.13	.07	.17	.10	-.44**	-.27*	-.30**	-.04
	FC	93	.99**	-.04	-.15	-.38**	-.12	-.13	.10	.30**	.30**	.08
AB/2*ATL	Y	79	1.00**	-.02	.07	-.04	.13	-.15	-.27**	-.31**	-.26**	.23*
	FC	95	1.00**	-.26**	.23*	-.02	.04	.04	.03	-.22*	-.18	-.04
2*AB/NP	Y	75	1.00**	-.02	.05	.12	-.06	-.15	-.06	-.04	-.05	-.18
	FC	89	.98**	.14	-.04	-.48**	-.26*	.30**	.44**	.29**	.37**	-.01
AB/2*NP	Y	67	1.00**	-.12	.22	.16	.27*	-.13	-.22	-.21	-.25*	.11
	FC	81	.99**	.24*	-.01	-.25*	.11	.05	.07	.07	.08	.00
2*ATL/NP	Y	73	.95**	-.20	-.10	-.03	-.24*	.15	-.20	-.13	-.08	.10
	FC	93	1.00**	-.15	.18	-.02	.10	-.03	.08	-.27**	-.19	.09
ATL/2*NP	Y	26	.99**	-.20	.23	-.07	.03	-.07	-.22	-.19	-.21	-.02
	FC	86	.99**	-.27**	.16	-.35**	.16	-.28**	.12	.01	.01	.07

Table 9. (Continued)

Population	Loc	n	Lysine (% protein) vs. Adj. lys %	Lys % dry wt	Plant yield	Kernel weight	Plant ht	Kernel size	Shrivel type	Shrivel freq	Shrivel index	Comp. factor
F_2's:												
AB/ATL	Y	150	.99**	-.20*	.16*	.07	.06	-.07	-.15	-.15	-.24**	.00
	FC	183	1.00**	-.25**	-.11	-.44**	-.07	-.12	.21**	.27**	.30**	.10
AB/NP	Y	147	.99**	-.06	.13	.20*	-.04	.10	-.11	-.23**	-.24**	-.04
	FC	184	.98**	-.25**	.06	-.22**	-.04	-.07	-.08	-.01	-.04	.02
ATL/NP	Y	151	.99**	-.17*	.10	.12	.16*	-.02	-.18*	-.06	-.08	.05
	FC	181	1.00**	-.01	-.02	-.38**	-.22**	-.13	.24**	.15*	.21**	.03
Among all individual plants	Y	1253	.99**	.06*	.02	-.15**	-.06*	-.11**	-.23**	-.25**	-.24**	-.03
	FC	1647	1.00**	-.21**	-.21**	-.52**	-.33**	-.29**	.08**	.06*	.08**	.00

*Indicates significance at the 5% level.
**Indicates significance at the 1% level.

Lysine content and adjacent plant competition were not associated with each other among all individual plants.

Gene Effects

Protein. Hayman's three parameter and six parameter models were employed to describe gene effects for protein and lysine percent of protein. In this model the sign of additive effects is a result of the estimators P_1-P_2. P_1-P_2 was used in all crosses as opposed to P_2-P_1. P_1 in all crosses of this study is the first parent in the pedigree and P_2 is the second parent. The magnitude of a generally reflects the magnitude of difference between the two parental means (Sun et al., 1972; Chapman and McNeal, 1970). The sign of the dominance effect is a function of the relationship of the F_1 to the mid-parent and indicates which parent may be contributing dominance variation.

Estimates of gene effects for protein are given in Table 10. Only the April Bearded/Nap Hal cross grown at Yuma gave a satisfactory fit for the three-parameter model. At Fort Collins, this cross had a significant chi-square value for the three-parameter model. For the crosses April Bearded/Atlas 66 and Atlas 66/Nap Hal, all chi-square values for the three-parameter model were significant. Therefore, significant epistatic effects for the inheritance of grain protein were detected in these crosses.

The cross April Bearded/Atlas 66 had large additive effects in the six-parameter model at both Yuma and Fort Collins. Dominance effects at Yuma were large and negative in sign suggesting that dominance is from Atlas 66. At Fort Collins, dominance was of little importance. Epistatic effects at Yuma and Fort Collins were of similar magnitude but were opposite in sign.

Table 10. Estimates of genetic effects and their standard errors by the weighted three-parameter and six-parameter models for protein in three wheat crosses grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Cross	Location	Genetic model and SE	Gene effects m	a	d	aa	ad	dd	Chi square	P
April Bearded/Atlas 66	Yuma	3PM	18.83	- .12	- .49				14.2	<.005
		SE	.07	.11	.21					
		6PM	18.78	- .95	-1.46	-1.08	- .97	3.12		
		SE	.12	.29	.79	.76	.31	1.33		
	Fort Collins	3PM	18.61	-2.19	- .96				10.9	.025-.010
		SE	.07	.12	.17					
		6PM	18.55	-1.45	.25	1.19	.87	-2.38		
		SE	.15	.29	.86	.85	.32	1.36		
April Bearded/Nap Hal	Yuma	3PM	19.73	- .57	- .48				4.9	.250-.100
		SE	.07	.13	.21					
		6PM	19.87	- .08	-1.12	- .61	.59	.34		
		SE	.16	.31	.90	.87	.34	1.43		
	Fort Collins	3PM	16.48	- .21	-1.13				9.0	.050-.025
		SE	.05	.09	.14					
		6PM	16.57	- .31	- .69	.48	- .06	-1.80		
		SE	.12	.21	.66	.64	.23	1.00		
Atlas 66/Nap Hal	Yuma	3PM	19.13	- .61	-1.48				26.3	<.005
		SE	.08	.12	.22					
		6PM	19.47	.99	-5.99	-4.41	1.69	7.26		
		SE	.14	.41	1.04	1.01	.43	1.83		
	Fort Collins	3PM	18.48	2.12	-1.78				13.6	<.005
		SE	.06	.09	.15					
		6PM	18.94	1.95	-3.08	-1.21	.13	.01		
		SE	.17	.26	.87	.85	.28	1.28		

April Bearded/Nap Hal at Yuma gave a low chi-square value which indicates a good fit for the three-parameter model. Epistasis was not identified in the six-parameter model. Additive gene action was most important, although a large dominance contribution for high protein from Nap Hal was indicated. The same cross at Fort Collins for the three-parameter model indicated that digenic epistasis may exist. However, significant epistasis was not found in the six-parameter model. Failure to fit the digenic epistasis model may indicate either trigenic epistasis, linkage or both.

The cross Atlas 66/Nap Hal, failed to fit the three-parameter model at both locations. At Yuma, dominance effects were more important than additive effects. All epistatic effects were greater than their standard errors, especially dd. The six-parameter model at Fort Collins had large positive additive effects. Large dominance effects were presumably from Nap Hal. Additive by additive epistasis was the most important kind of epistasis. Nap Hal in this cross caused contrasting dominance effects. At Yuma, these dominance effects were for higher protein while at Fort Collins Nap Hal had dominance effects for low protein content.

Lysine. All crosses at each location failed to satisfactorily fit the three-parameter model (Table 11). April Bearded/Atlas 66 exhibited large additive effects in the six-parameter model at both Yuma and Fort Collins. At Fort Collins, dominance effects were important while at Yuma dominance effects were of little consequence. All three types of epistasis were important at Fort Collins while only ad and dd were important at Yuma.

The six-parameter model indicated epistatic gene effects at Yuma and Fort Collins for the cross April Bearded/Nap Hal. At Yuma the domin-

'able 11. Estimates of genetic effects and their standard errors by the weighted three-parameter and six-parameter models for lysine as a percent of protein in three wheat crosses grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Cross	Location	Genetic model and SE	Gene effects m	a	d	aa	ad	dd	Chi square	P
pril Bearded/Atlas 66	Yuma	3PM	2.869	.081	.054				19.2	<.005
		SE	.005	.007	.014					
		6PM	2.885	.128	.047	.013	.054	-.172		
		SE	.009	.022	.059	.057	.023	.099		
	Fort Collins	3PM	2.776	.183	-.037				9.3	.050-.025
		SE	.005	.007	.013					
		6PM	2.791	.142	-.146	-.105	-.050	.153		
		SE	.011	.018	.059	.058	.020	.089		
pril Bearded/Nap Hal	Yuma	3PM	2.968	-.070	-.019				12.3	.010-.005
		SE	.005	.007	.014					
		6PM	2.994	-.010	-.133	-.105	-.034	.063		
		SE	.011	.019	.059	.057	.020	.091		
	Fort Collins	3PM	3.045	-.032	.049				21.5	<.005
		SE	.005	.007	.014					
		6PM	3.036	-.071	.171	.138	-.042	-.286		
		SE	.010	.018	.055	.054	.020	.087		
tlas 66/Nap Hal	Yuma	3PM	2.902	-.141	.028				16.1	<.005
		SE	.005	.007	.014					
		6PM	2.875	-.170	.199	.156	-.031	-.138		
		SE	.009	.029	.070	.069	.030	.126		
	Fort Collins	3PM	2.852	-.217	.051				7.8	.100-.050
		SE	.004	.005	.011					
		6PM	2.866	-.187	-.033	.083	.033	.102		
		SE	.011	.017	.056	.055	.018	.084		

ance by dominance interaction was of little significance but at Fort Collins this was the largest epistasis component. Additive gene action at Yuma for this cross was insignificant but at Fort Collins additive effects were important. Dominance effects were important at both locations.

Epistatic gene effects for Atlas 66/Nap Hal were relatively small in comparison to their respective standard errors. Additive gene effects were the largest at both locations. Dominance gene effects were not significant at Fort Collins.

Heritability

Heritability estimates for protein and lysine percent of protein are given in Table 12. Negative estimates were computed for the Yuma location in two crosses. These negative estimates are due to large variance estimates in backcross and F_1 generations. Method III requires homogeneity of parental variances before pooling is valid. Where estimates are not given for Method III, parental variances were not homogenous as indicated by Bartlett's test.

All heritability estimates were positive at Fort Collins. The cross April Bearded/Nap Hal had the most consistent positive estimates at both locations.

Method I is a narrow sense estimate whereas Methods II and III are broad sense estimates. The difference between broad sense and narrow sense estimates should reflect the magnitude of dominance variance and epistatic variance. The narrow sense estimates calculated by Warner's method (Warner, 1952) were negative at Yuma for all crosses except April Bearded/Nap Hal. Warner's method assumes environmental variances

Table 12. Heritability estimates of protein and lysine as a percent of protein for three crosses grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

	Heritability estimate (%)					
	Method I[1]		Method II[2]		Method III[3]	
Cross	Yuma	Fort Collins	Yuma	Fort Collins	Yuma	Fort Collins
April Bearded/Atlas 66						
Protein	-58	14	- 8	73	29	31
Lysine	-82	70	- 1	57	34	
April Bearded/Nap Hal						
Protein	19	65	54	65	30	
Lysine	49	47	41	22	53	
Atlas 66/Nap Hal						
Protein	-15	81	- 8	75		
Lysine	-22	81	8	58	44	

1/ $H = \frac{2V_{F2} - (V_{BC1} + V_{BC2})}{V_{F2}} \cdot 100$

2/ $H = \frac{V_{F2} - V_{F1}}{V_{F2}} \cdot 100$

3/ $H = \frac{V_{F2} - (V_{P1} \cdot V_{P2})^{\frac{1}{2}}}{V_{F2}} \cdot 100$

in backcross and F_2 generations are comparable and epistatic variability is negligible. These assumptions may have been violated in these crosses.

At Fort Collins, the cross April Bearded/Atlas 66 had a narrow sense estimate of 14% for protein compared to 73% and 31% for broad sense estimates. This indicates that additive variation was less than half the total genetic variation.

The narrow sense estimate at Fort Collins for protein in April Bearded/Nap Hal was equal to the broad sense estimate. However, at Yuma, the narrow sense estimate for this cross was 19% versus 54% and 30% for broad sense estimates.

Protein heritability estimated in the narrow sense at Fort Collins for Atlas 66/Nap Hal was larger than the broad sense estimate. This suggests that nearly all of the heritable portion of the variation is additive and fixable.

Narrow sense estimates for lysine content in all crosses grown at Fort Collins were larger than broad sense estimates. In the April Bearded/Nap Hal cross at Yuma, the narrow sense estimate was larger than the one broad sense estimate and 4% less than the other broad sense estimate. No comparisons between narrow sense and broad sense heritiabilities in the April Bearded/Atlas 66 and Atlas 66/Nap Hal populations could be made at Yuma because the narrow sense estimates were negative.

DISCUSSION

This investigation was designed to study the performance and inheritance of grain protein and lysine in three wheat crosses with high protein parents. Individual plants of the parents, the F_1 generations, and segregating progenies were grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Plant to plant variance in homogeneous populations is considered environmental or nongenetic. Between plant variances in segregating progenies are genetic and environmental in origin. Between plant variances of parents and F_1 generations were generally large for both protein and lysine and sometimes greater than the segregating progeny variances. The variation in parental and F_1 populations may be attributed to nonhomozygous parents or to environmental influences. Parents utilized in this study originated from selfed plants grown in the greenhouse. It is most likely that the magnitude of these variances is due to environmental causes rather than nonhomozygous parents.

Several environmental factors can influence the phenotypic expression of a genotype. Visual observation of the Yuma nursery at maturity indicated plant heights were highly variable within nonsegregating rows. This observation was supported by the large measured variability for plant height (Table A7). Significant negative correlations were detected between plant height and protein content in several nonsegregating populations. Between plant variances were determined by a nested analysis of variance to remove replication and plot sources of variation. Comparison of between plant variances (Table 5) and population variances without replication and plot effects considered (Table A1-2) indicate considerable

variation was removed by accounting for these effects at Yuma. The variation could possibly be attributed to poor emergence and seedling vigor since some shriveled seeds were planted. It is also possible that the variation can be attributed to microenvironment influences such as a soil fertility or soil moisture gradient in the nursery.

Since several plants were missing at Yuma, harvested plants were scored for adjacent plant competition to determine its influence on protein and lysine (percent of protein). No definite relationships could be established between adjacent plant competition and percent protein or lysine as a percent of protein.

The Fort Collins nursery appeared uniform throughout the growing season. Quality of seed planted at Fort Collins was similar to the seed planted at Yuma. Plant height variability was low in nonsegregating populations (Table A7). Replication effects were small in comparison to the Yuma nursery. Problems were encountered when an epidemic of leaf and stem rust developed in this nursery late in the growing season. Genotype responses to those diseases were different. Atlas 66 expressed resistance to both stem and leaf rust. April Bearded showed moderate resistance to stem rust and susceptibility to leaf rust. Nap Hal was susceptible to both leaf and stem rust. Since Nap Hal matured earlier than the other parents it may have partially escaped disease infection.

In addition to large environmental variances at each location, genotype by location interactions were found for protein and lysine. Genotypic background and adaptability of the parents may have contributed to their different performances at Yuma and Fort Collins. Although heading and maturity data were not obtained, maturity differences were evident. The latest maturing parent was Atlas 66 which has intermediate

growth habit. Of the two spring wheats, Nap Hal matures earlier than April Bearded. These differences in growth habit and maturity could have influenced protein expression.

Since measurements for each plant were taken for yield per plant, kernel weight, and shriveling, protein values could be adjusted for these characteristics. Nonsegregating progeny data were utilized to compute a multiple regression equation for protein with three independent variables: (1) plant yield, (2) kernel weight, and (3) shriveling index. The multiple regression equation accounted for 37.7% of the variation in protein of nonsegregating populations at Yuma and 25.4% at Fort Collins. All protein values at a location were adjusted by the multiple regression equation for that location. Between plant variances were still large in nonsegregating populations relative to between plant variances of segregating populations. Heritability estimates for adjusted protein generally were not improved. The major improvement from adjustment was for the Atlas 66/Nap Hal cross at Yuma. Estimates for this cross were 73%, 44%, and 65% by Method I, Method II, and Method III, respectively.

Plant breeders have used the principle of transgressive segregation to obtain superior segregates for quantitative traits. Transgressive segregation occurs when progeny arise by segregation outside the range of the parents. Johnson et al. (1973a) reported transgressive segregation for low and high protein of F_2-derived bulks of Atlas 66/Nap Hal. Apparent transgressive segregation also occurred in this study. The range of the F_2 plants of Atlas 66/Nap Hal was 1.2 percentage points beyond the range of the parents for high and low protein at Yuma (Table A1). At Fort Collins transgressive segregation occurred for low protein.

The F_2 range was 1.5 percentage points below the parental range.

Transgressive segregation also appeared in the April Bearded/Atlas 66 and April Bearded/Nap Hal crosses. The F_2 generation range of April Bearded/Atlas 66 was 1.4 and 0.50 percentage points beyond the low range of the parents at Yuma and Fort Collins, respectively. No significant transgressive segregation for high protein occurred for this cross. Differences in range values for the April Bearded/Nap Hal cross were found for high protein. The range of the F_2 was 1.4 and 0.7 percentage points higher than the parental range at Yuma and Fort Collins, respectively.

The only substantial difference between parent and F_2 range values for lysine (percent of protein) appeared in the Atlas 66/Nap Hal cross. At Yuma the F_2 range was 0.30 percentage points below the parents and at Fort Collins the F_2 range was 0.22 percentage points above the parental range.

Gene effects as measured by Hayman's model indicated the mode of inheritance for protein and lysine could not be described simply by additive and dominance gene action. All crosses except April Bearded/Nap Hal at Yuma failed to fit the three-parameter model for protein inheritance. For lysine inheritance, all crosses failed to fit the three-parameter model. In some cases digenic epistatic estimates were large while in others they were small. The small estimates suggest trigenic epistasis, linkage, or both are involved in protein and lysine inheritance.

General interpretations of the mode of protein and lysine inheritance in this study are complicated by the genotype-location interaction. The results indicate epistasis may be an important contributor to genetic variation. Chapman and McNeal (1970), however, have reported significant

epistasis to be absent in five wheat crosses analyzed for grain protein. Busch, Janke, and Frohberg (1974) have suggested additive by additive interactions and higher order additive interactions may be more pronounced in wheat because its hexaploid nature possibly enhances epistatic variances by intergenomic interactions.

Additive gene action was generally important in protein and lysine inheritance. Dominance effects were also present, especially for protein. F_1 hybrid means were always below mid-parent values, near the low-protein parent, or below the low-protein parent. The low protein performance of the F_1 generations may be associated with a heterotic effect for plant yield. The F_1 hybrid plant yields were as much as 25% higher than the high-yielding parent at Yuma and at Fort Collins, F_1 yields were as much as 40% more than the high-yielding parent. Heterosis for yield may be expected since the parent genotypes represent diverse germ plasm. Allan and Rubenthaler (1972) have reported that high flour protein tended to be recessively inherited. Twenty percent of the hybrids they studied had flour proteins below their low parent.

Heritability estimates in the broad and narrow sense were inconsistent across locations. Estimates at Fort Collins were positive for all methods of heritability estimation. Negative estimates were reported for April Bearded/Atlas 66 and Atlas 66/Nap Hal at Yuma. The April Bearded/Nap Hal cross had positive estimates for both protein and lysine at Yuma and Fort Collins which suggests this population may be of value for further selection.

Estimates of gene action and heritability may be different under other spacings and plant population densities. Clement (1972) evaluated wheat hybrids and varieties using a systematic spacing design. He found

population density significantly affected all characters measured. Yield per plant, spikes per plant, seed weight, seed per spike, number of days from planting to anthesis, and length of grain fill increased as population level decreased. He suggested that data from individual plants may not give reliable information of the gene action involved in crosses.

Hanson (1963) has questioned the value of describing genetic variability based on individually spaced plants. He believes the phenotypic expression of a genotype under space planting cannot be projected to that expected for normal competing conditions in a drilled row. Furthermore, he stated that estimates of environmental variability are not entirely reliable.

The magnitude of environmental variances in nonsegregating spaced plants can exceed segregating progeny variances for a quantitative trait such as protein. A more practical approach may be to examine genetic and nonheritable variation in drilled rows of F_2 plant progenies or advanced lines.

Heritability, however, was originally defined in terms of the individual organism. Heritability estimates for plant characters are useful to appraise the magnitude of genetic variation. Plant breeders should realize that estimates may be biased by genotype-environment interactions.

Results of this study indicate that low protein is dominant to high protein and several genes are involved. High protein is probably the accumulation of favorable recessive genes. Epistatic gene action may also be involved. For these reasons, selection for high protein probably should be delayed until the F_3 or later generations. By delaying

selection, favorable recessive genes would be fixed and desirable epistatic combinations would be possible.

In rice, Hillerislambers et al. (1973) found low protein to be dominant and heritabilities to be low. The authors have suggested two breeding procedures to be utilized to develop high protein rice lines. The methods they proposed were single seed descent with rapid generation advancement and a bulking system which allows equal contribution of all genotypes to succeeding generations.

Rice breeders at IRRI (International Rice Research Institute, 1973) have also found evidence that suggests several dominant alleles control low protein and the cumulative action of recessive genes cause high protein. They are utilizing Jensen's diallel selective mating system to improve rice protein content.

Interpretation of the results in this study indicate that the above-mentioned breeding procedures or recurrent selection would be valuable in breeding for high protein and lysine in wheat. Breeding for high protein content in wheat by the pedigree system would be very costly. Kumar (1973) has estimated that twice as many resources are required to develop and test pedigree lines for yield as with single seed descent.

Modifications of the pedigree system such as single seed descent may have merit. A modification of the pedigree system with progeny bulks could be utilized. A large population of F_2 spaced plants could be grown at Yuma, Arizona, where high plant yields could be obtained. With a large quantity of seed for each plant, several progeny rows from one plant could be planted. Since environmental considerations are important, F_2-derived bulks should be replicated and grown at two or more locations. Several rows of parents and control varieties should be included in the

F_2-derived bulk nursery. All F_2-derived bulks in the F_3 generation would be harvested and grain evaluated for protein and lysine content. Superior F_2-derived bulks could be selected and further evaluated. Selection within bulks could be done on a single seed or head basis. Advantages of this procedure are early generation evaluation, minimal labor for evaluation, and the selection unit would be drilled progeny rows which are more representative of cultural practices.

SUMMARY

Three high protein wheats, April Bearded (C.I. 7337), Atlas 66 (C.I. 12561), and Nap Hal (P.I. 176217) were crossed in diallel fashion without reciprocals. Earlier studies indicated April Bearded and Nap Hal possess higher than normal levels of lysine. Parents, F_1, F_2 and backcross populations were grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Data were obtained for grain protein, lysine as a percent of protein, adjusted lysine, lysine percent on a dry weight basis, plant yield, kernel weight, kernel size, shriveling type, shriveling frequency, shriveling index, and competition between adjacent plants. Means, variances, and correlations were computed to determine gene effects, heritabilities, and correlated responses.

Environmental variances computed from nonsegregating populations were large. Both narrow and broad heritability estimates were variable which reflects the precision of estimation for environmental variances. Genotype-environment interactions may bias heritability estimates. Significant genotype-location interactions were observed for protein and lysine.

Protein and lysine were inherited in a quantitative manner. Analyses of gene effects by Hayman's model suggests additive, dominance, and epistasis gene action. Generally, additive gene effects were more consistent and important.

Data from this study indicate that Atlas 66 has major genes for protein which were stable over environments. Genes for high protein from April Bearded and Nap Hal were not stable over environments. April

Bearded has major genes for high protein which are in common with genes from Nap Hal. Minor gene differences between April Bearded and Nap Hal exist. Nap Hal probably has major genes different from Atlas 66. Gene differences between April Bearded and Atlas 66 were detected.

Nap Hal and April Bearded possess genes for high lysine (percent of protein). Atlas 66 has a low lysine level. High lysine genes from April Bearded and Nap Hal are different, although, some genes may be in common. Expression of high lysine was relatively stable over environments.

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APPENDIX

Table A1. Means, variances, ranges, and coefficients of variation for percent grain protein of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

	Yuma						Fort Collins					
				Range		CV				Range		CV
Population	n	Mean	Variance	Low	High	%	n	Mean	Variance	Low	High	%
Parents:												
AB	69	19.23	3.5283	15.1	24.2	9.8	92	16.69	3.1812	13.9	23.6	10.7
ATL	63	19.18	1.6903	15.3	22.0	6.8	97	21.35	2.9508	18.0	26.2	8.0
NP	63	20.58	4.3559	16.3	24.2	10.1	93	17.19	.6544	15.7	20.9	4.7
F_1's:												
AB/ATL	71	18.83	3.2248	13.7	23.6	9.5	91	18.08	1.2489	16.1	20.7	6.2
AB/NP	72	19.40	2.0608	16.2	23.9	7.4	99	15.77	.9877	14.2	20.5	6.3
ATL/NP	77	18.29	3.4405	13.6	22.9	10.1	90	17.40	1.3166	15.8	24.6	6.6
BC's:												
2*AB/ATL	70	18.03	5.7358	12.6	24.3	13.3	93	18.12	4.0148	14.3	24.2	11.1
AB/2*ATL	79	18.98	2.0531	15.1	22.2	7.6	95	19.57	4.2840	16.2	25.9	10.6
2*AB/NP	75	19.68	2.5750	15.2	24.4	8.2	89	16.53	2.8080	13.6	23.5	10.1
AB/2*NP	67	19.76	4.0655	15.4	24.2	10.2	81	16.84	1.4785	14.9	21.6	7.2
2*ATL/NP	73	18.87	4.2400	12.9	25.4	10.9	93	19.61	3.9814	15.2	25.4	10.2
ATL/2*NP	26	17.88	3.8506	14.2	21.2	11.0	86	17.66	3.0847	14.5	25.6	9.9
F_2's:												
AB/ATL	150	18.78	2.6254	13.7	23.3	8.6	183	18.55	4.6402	14.7	26.4	11.6
AB/NP	147	19.87	3.6186	14.9	25.6	9.6	184	16.57	2.7594	13.4	24.3	10.0
ATL/NP	151	19.50	3.8229	13.9	25.4	10.0	181	18.94	5.1558	14.4	25.9	12.0

Table A2. Means, variances, ranges, and coefficients of variation for lysine as a percent of protein of 15 populations grown at Yuma Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean	Variance	Range Low	Range High	CV %	n	Mean	Variance	Range Low	Range High	CV %
Parents:												
AB	69	2.90	.0160	2.53	3.20	4.4	92	2.99	.0243	2.62	3.39	5.2
ATL	63	2.76	.0077	2.58	2.99	3.2	97	2.60	.0090	2.41	2.88	3.6
NP	63	3.04	.0163	2.68	3.44	4.2	93	3.05	.0057	2.84	3.23	2.5
F_1's:												
AB/ATL	71	2.87	.0197	2.60	3.29	4.9	91	2.75	.0136	2.46	3.05	4.2
AB/NP	72	2.94	.0103	2.60	3.13	3.4	99	3.05	.0178	2.54	3.42	4.4
ATL/NP	77	2.94	.0148	2.63	3.37	4.1	90	2.88	.0132	2.47	3.22	4.0
BC's:												
2*AB/ATL	70	2.95	.0294	2.63	3.37	5.8	93	2.84	.0195	2.49	3.22	4.9
AB/2*ATL	79	2.82	.0212	2.34	3.17	5.2	95	2.69	.0134	2.48	2.95	4.3
2*AB/NP	75	2.92	.0156	2.67	3.22	4.3	89	3.03	.0188	2.67	3.30	4.5
AB/2*NP	67	3.02	.0190	2.66	3.45	4.6	81	3.11	.0144	2.75	3.38	3.9
2*ATL/NP	73	2.83	.0115	2.63	3.22	3.8	93	2.75	.0148	2.48	3.09	4.4
ATL/2*NP	26	3.00	.0269	2.65	3.30	5.5	86	2.94	.0206	2.54	3.33	4.9
F_2's:												
AB/ATL	150	2.89	.0131	2.65	3.23	4.0	183	2.79	.0261	2.39	3.26	5.8
AB/NP	147	2.99	.0162	2.70	3.48	4.3	184	3.04	.0180	2.71	3.43	4.4
ATL/NP	151	2.87	.0178	2.33	3.29	4.7	181	2.87	.0240	2.44	3.45	5.4

Table A3. Means, variances, ranges, and coefficients of variation for adjusted lysine percent of protein of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean	Variance	Range Low	Range High	CV %	n	Mean	Variance	Range Low	Range High	CV %
Parents:												
AB	69	3.10	.0164	2.73	3.37	4.1	92	2.99	.0243	2.62	3.39	5.2
ATL	63	2.97	.0082	2.77	3.21	3.1	97	2.60	.0090	2.41	2.88	3.6
NP	63	3.24	.0176	2.86	3.63	4.1	93	3.05	.0057	2.84	3.23	2.5
F_1's:												
AB/ATL	71	3.07	.0175	2.78	3.48	4.3	91	2.97	.0133	2.66	3.25	3.9
AB/NP	72	3.15	.0108	2.82	3.34	3.3	99	3.23	.0170	2.71	3.63	4.0
ATL/NP	77	3.14	.1148	2.84	3.46	3.7	90	3.09	.0130	2.68	3.43	3.7
BC's:												
2*AB/ATL	70	3.14	.0214	2.83	3.46	4.7	93	3.04	.0197	2.67	3.42	4.6
AB/2*ATL	79	3.02	.0216	2.55	3.39	4.9	95	2.90	.0153	2.66	3.17	4.3
2*AB/NP	75	3.12	.0161	2.88	3.43	4.1	89	3.22	.0168	2.88	3.52	4.0
AB/2*NP	67	3.22	.0198	2.86	3.66	4.4	81	3.31	.0135	2.96	3.57	3.5
2*ATL/NP	73	3.03	.0089	2.80	3.30	3.1	93	2.95	.0157	2.66	3.26	4.2
ATL/2*NP	26	3.20	.0251	2.85	3.46	5.0	86	3.15	.0199	2.73	3.49	4.5
F_2's:												
AB/ATL	150	3.09	.0128	2.82	3.42	3.7	183	2.99	.0262	2.57	3.44	5.4
AB/NP	147	3.20	.0173	2.88	3.64	4.1	184	3.23	.0147	2.92	3.55	3.8
ATL/NP	151	3.07	.0173	2.51	3.42	4.3	181	3.07	.0245	2.62	3.60	5.1

Table A4. Means, variances, ranges, and coefficients of variation for lysine percent on a dry weight basis of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean	Variance	Range Low	Range High	CV %	n	Mean	Variance	Range Low	Range High	CV %
Parents:												
AB	69	.55	.001849	.44	.68	7.8	92	.49	.001790	.43	.68	8.6
ATL	63	.52	.000867	.44	.59	5.6	97	.55	.001367	.48	.68	6.7
NP	63	.62	.003024	.52	.78	8.8	93	.52	.000520	.48	.62	4.4
F_1's:												
AB/ATL	71	.53	.001470	.43	.63	7.2	91	.49	.000590	.44	.55	4.9
AB/NP	72	.57	.001666	.49	.68	7.2	99	.48	.000949	.38	.58	6.5
ATL/NP	77	.53	.001895	.42	.65	8.2	90	.50	.000950	.44	.65	6.2
BC's:												
2*AB/ATL	70	.52	.002469	.42	.65	9.5	93	.51	.002484	.41	.73	9.8
AB/2*ATL	79	.53	.000906	.44	.63	5.7	95	.52	.001992	.41	.66	8.6
2*AB/NP	75	.57	.001604	.47	.67	7.0	89	.50	.002365	.42	.69	9.8
AB/2*NP	67	.59	.002823	.45	.70	9.0	81	.52	.001364	.46	.65	7.1
2*ATL/NP	73	.53	.002867	.38	.70	10.1	93	.53	.002125	.45	.65	8.6
ATL/2*NP	26	.53	.002183	.41	.61	8.8	86	.51	.001364	.45	.65	7.2
F_2's:												
AB/ATL	150	.54	.001458	.43	.63	7.1	183	.51	.001985	.41	.66	8.7
AB/NP	147	.59	.002584	.48	.82	8.6	184	.50	.001522	.42	.68	7.8
ATL/NP	151	.55	.002191	.44	.69	8.5	181	.54	.003249	.41	.74	10.6

Table A5. Means, variances, ranges and coefficients of variation for yield per plant of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

	Yuma						Fort Collins					
		Mean		Range		CV		Mean		Range		CV
Population	n	grams	Variance	Low	High	%	n	grams	Variance	Low	High	%
Parents:												
AB	69	30.6	192.30	5.0	59.0	45.3	92	18.2	34.82	5.0	31.0	32.4
ATL	63	37.1	360.41	5.0	86.0	51.2	97	19.8	29.21	7.0	32.0	27.4
NP	63	22.9	167.04	5.0	63.0	56.3	93	16.5	14.03	8.0	29.0	22.7
F_1's:												
AB/ATL	71	35.8	574.53	5.0	102.0	66.9	91	27.7	64.58	7.0	57.0	29.1
AB/NP	72	38.3	382.73	7.0	85.0	51.1	99	20.2	25.58	8.0	42.0	25.0
ATL/NP	77	38.8	543.21	5.0	98.0	60.1	90	24.4	24.78	8.0	36.0	20.4
BC's:												
2*AB/ATL	70	30.2	289.20	5.0	85.0	56.3	93	19.4	63.68	6.0	43.0	41.1
AB/2*ATL	79	33.5	268.92	5.0	68.0	48.9	95	22.9	60.78	5.0	42.0	34.1
2*AB/NP	75	32.3	400.70	5.0	81.0	62.0	89	16.4	30.30	7.0	33.0	33.5
AB/2*NP	67	29.3	456.40	5.0	89.0	73.0	81	15.8	19.83	7.0	28.0	28.2
2*ATL/NP	73	36.8	447.28	6.0	108.0	57.4	93	19.4	32.26	8.0	32.0	29.3
ATL/2*NP	26	38.5	407.70	5.0	70.0	52.4	86	18.4	43.35	5.0	44.0	35.8
F_2's:												
AB/ATL	150	38.1	401.26	5.0	99.0	52.6	183	23.1	62.23	6.0	61.0	34.1
AB/NP	147	30.7	308.05	5.0	104.0	57.2	184	16.9	21.87	5.0	29.0	27.7
ATL/NP	151	35.4	441.19	5.0	118.0	59.4	181	17.4	42.05	5.0	35.0	37.2

Table A6. Means, variances, ranges, and coefficients of variation for kernel weight of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean mg	Variance	Range Low	Range High	CV %	n	Mean mg	Variance	Range Low	Range High	CV %
Parents:												
AB	69	33.4	21.58	21.0	54.0	13.9	92	25.70	8.30	17.8	32.7	11.2
ATL	63	35.6	11.94	26.4	45.3	9.7	97	28.10	10.23	18.7	34.8	11.4
NP	63	21.9	14.92	14.1	29.8	17.6	93	20.73	2.19	17.9	24.5	7.1
F_1's:												
AB/ATL	71	36.0	21.00	23.1	44.3	12.7	91	33.78	7.90	26.9	43.4	8.3
AB/NP	72	30.6	20.26	20.1	43.9	14.7	99	25.43	5.55	17.8	30.1	9.3
ATL/NP	77	33.4	15.29	23.3	41.0	11.7	90	28.54	4.30	17.9	33.2	7.3
BC's:												
2*AB/ATL	70	35.9	19.60	22.1	46.4	12.3	93	29.03	16.90	17.4	38.6	14.2
AB/2*ATL	79	36.2	16.31	21.2	48.1	11.2	93	30.66	14.57	20.3	37.9	12.4
2*AB/NP	75	31.5	18.54	20.3	40.6	13.7	89	24.86	13.24	15.7	36.2	14.6
AB/2*NP	67	27.7	23.08	16.1	37.4	17.3	81	20.96	8.64	13.1	27.3	14.0
2*ATL/NP	73	34.4	18.33	21.4	41.7	12.5	93	26.99	14.16	18.1	34.9	13.9
ATL/2*NP	26	30.0	18.29	19.4	38.7	14.2	86	24.02	13.30	15.2	32.1	15.2
F_2's:												
AB/ATL	150	36.5	15.45	21.3	45.3	10.8	183	29.73	23.60	15.7	42.7	16.3
AB/NP	147	28.0	17.86	17.3	39.0	15.1	184	23.85	9.41	15.6	31.9	12.9
ATL/NP	151	29.8	21.96	17.3	39.4	15.7	181	25.21	17.49	14.5	33.4	16.6

Table A7. Means, variances, ranges, and coefficients of variation for plant height of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean cm	Variance	Range Low	Range High	CV %	n	Mean cm	Variance	Range Low	Range High	CV %
Parents:												
AB	69	140.8	324.10	92.0	165.0	12.8	92	106.3	38.46	90.0	120.0	5.8
ATL	63	128.2	667.83	92.0	157.0	20.2	97	100.7	33.66	90.0	120.0	5.7
NP	63	114.2	131.28	90.0	134.0	10.0	93	76.4	29.32	65.0	95.0	7.1
F_1's:												
AB/ATL	71	145.9	182.76	115.0	166.0	9.3	91	112.2	28.51	100.0	125.0	4.8
AB/NP	72	142.7	177.52	100.0	166.0	9.3	99	97.0	44.29	75.0	110.0	6.9
ATL/NP	77	135.9	150.98	98.0	160.0	9.0	90	95.7	43.57	70.0	110.0	6.9
BC's:												
2*AB/ATL	70	146.9	218.79	115.0	174.0	10.1	93	109.8	73.07	75.0	130.0	7.8
AB/2*ATL	79	143.8	150.43	110.0	165.0	8.5	95	105.5	57.97	85.0	120.0	7.2
2*AB/NP	75	141.3	172.10	101.0	165.0	9.3	89	103.0	85.64	75.0	120.0	9.0
AB/2*NP	67	126.9	162.94	92.0	150.0	10.1	81	85.4	42.62	70.0	100.0	7.6
2*ATL/NP	73	129.3	202.51	91.0	160.0	11.0	93	100.7	53.44	85.0	125.0	7.3
ATL/2*NP	26	131.5	113.94	110.0	150.0	8.1	86	83.0	33.75	65.0	95.0	7.0
F_2's:												
AB/ATL	150	148.0	161.83	110.0	175.0	8.6	183	107.5	83.09	75.0	125.0	8.5
AB/NP	147	136.6	152.41	105.0	164.0	9.0	184	94.6	55.49	75.0	115.0	7.9
ATL/NP	151	128.8	159.61	75.0	158.0	9.8	181	90.8	134.14	60.0	125.0	12.8

Table A8. Means, variances, ranges, and coefficients of variation for shrivel index of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean*	Variance	Range Low	Range High	CV %	n	Mean*	Variance	Range Low	Range High	CV %
Parents:												
AB	69	7.7	43.24	2.0	28.0	85.3	92	18.5	60.58	6.0	36.0	42.0
ATL	63	13.1	35.68	3.0	24.0	45.6	97	19.4	64.34	3.0	36.0	41.4
NP	63	10.7	95.29	0.0	32.0	91.2	93	13.0	36.24	3.0	32.0	46.5
F_1's:												
AB/ATL	71	12.4	46.25	1.0	32.0	54.7	91	11.3	27.79	3.0	21.0	46.7
AB/NP	72	7.0	50.85	1.0	28.0	101.7	99	12.6	42.25	2.0	36.0	51.6
ATL/NP	77	8.0	35.28	1.0	24.0	74.4	90	11.7	32.93	3.0	36.0	49.0
BC's:												
2*AB/ATL	70	7.7	34.55	2.0	24.0	76.2	93	16.8	68.66	3.0	36.0	49.4
AB/2*ATL	79	10.6	54.30	0.0	36.0	69.6	95	14.1	57.99	3.0	36.0	53.8
2*AB/NP	75	10.1	65.51	1.0	27.0	80.3	89	17.7	63.85	2.0	36.0	45.2
AB/2*NP	67	9.0	54.92	0.0	36.0	82.2	81	21.7	76.10	6.0	36.0	40.3
2*ATL/NP	73	11.0	74.71	0.0	36.0	78.3	93	17.3	73.24	6.0	36.0	49.4
ATL/2*NP	26	6.1	29.43	0.0	18.0	89.3	86	14.2	63.06	2.0	36.0	55.7
F_2's:												
AB/ATL	150	8.4	46.24	0.0	36.0	81.4	183	14.7	62.35	2.0	36.0	53.6
AB/NP	147	8.6	62.85	0.0	36.0	91.8	184	17.2	47.38	2.0	36.0	40.0
ATL/NP	151	12.1	71.99	0.0	36.0	70.0	181	18.4	65.98	2.0	36.0	44.0

*Measured on a scale of 0 to 45.

Table A9. Means, variances, ranges, and coefficients of variation for kernel size for 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean*	Variance	Range Low	Range High	CV %	n	Mean*	Variance	Range Low	Range High	CV %
Parents:												
A3	69	3.3	.23	2.0	4.0	14.5	92	3.0	.04	2.0	4.0	6.9
ATL	63	3.4	.25	3.0	4.0	9.3	97	3.3	.19	3.0	4.0	13.5
NP	63	2.6	.25	2.0	3.0	19.1	93	3.0	.01	2.0	3.0	3.5
F_1's:												
AB/ATL	71	3.3	.23	3.0	4.0	14.3	91	3.8	.17	3.0	4.0	10.8
AB/NP	72	3.2	.20	2.0	4.0	14.0	99	3.1	.06	3.0	4.0	9.3
ATL/NP	77	3.5	.28	2.0	4.0	15.1	90	3.2	.17	3.0	4.0	13.0
BC's:												
2*AB/ATL	70	3.4	.24	3.0	4.0	14.5	93	3.2	.19	2.0	4.0	13.5
AB/2*ATL	79	3.4	.24	3.0	4.0	14.4	95	3.4	.25	3.0	4.0	14.5
2*AB/NP	75	3.1	.17	2.0	4.0	13.0	89	3.0	.10	2.0	4.0	10.6
AB/2*NP	67	3.1	.34	2.0	4.0	19.0	81	3.0	.01	2.0	3.0	3.7
2*ATL/NP	73	3.3	.25	2.0	4.0	15.0	93	3.2	.18	3.0	4.0	13.2
ATL/2*NP	26	3.1	.35	2.0	4.0	18.9	86	3.1	.11	2.0	4.0	10.9
F_2's:												
AB/ATL	150	3.3	.23	2.0	4.0	14.4	183	3.3	.23	2.0	4.0	14.6
AB/NP	147	3.0	.12	2.0	4.0	11.4	184	3.0	.04	2.0	4.0	7.0
ATL/NP	151	3.1	.24	2.0	4.0	15.6	181	3.1	.18	2.0	4.0	13.8

*Measured on a scale of 1 to 5.

Table A10. Means, variances, ranges, and coefficients of variation for shrivel type of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean*	Variance	Range Low	Range High	CV %	n	Mean*	Variance	Range Low	Range High	CV %
Parents:												
AB	69	2.7	.26	2.0	4.0	18.8	92	3.3	.20	3.0	4.0	13.8
ATL	63	2.9	.07	2.0	3.0	9.3	97	3.2	.18	3.0	4.0	13.2
NP	63	2.6	.46	1.0	5.0	25.6	93	3.1	.10	2.0	4.0	10.3
F_1's:												
AB/ATL	71	2.8	.26	1.0	4.0	18.5	91	3.0	.02	2.0	4.0	5.0
AB/NP	72	2.3	.67	1.0	4.0	35.4	99	3.1	.11	2.0	4.0	10.7
ATL/NP	77	2.7	.27	1.0	4.0	19.6	90	3.0	.04	2.0	4.0	7.0
BC's:												
2*AB/ATL	70	2.7	.21	2.0	3.0	16.8	93	3.2	.16	3.0	4.0	12.7
AB/2*ATL	79	2.7	.38	1.0	4.0	23.2	95	3.2	.15	3.0	4.0	12.1
2*AB/NP	75	2.7	.33	1.0	4.0	21.4	89	3.2	.19	2.0	4.0	13.7
AB/2*NP	67	2.6	.51	0.0	4.0	27.2	81	3.4	.27	3.0	5.0	15.2
2*ATL/NP	73	2.8	.38	1.0	4.0	21.9	93	3.3	.22	3.0	4.0	14.1
ATL/2*NP	26	2.5	.42	1.0	4.0	25.9	86	3.2	.19	2.0	4.0	13.8
F_2's:												
AB/ATL	150	2.6	.44	1.0	4.0	25.3	183	3.0	.12	2.0	4.0	11.3
AB/NP	147	2.6	.47	1.0	4.0	26.2	184	3.0	.08	2.0	4.0	9.1
ATL/NP	151	2.9	.35	1.0	4.0	20.6	181	3.2	.16	2.0	4.0	12.9

*Measured on a scale of 1 to 5.

Table A11. Means, variances, ranges and coefficients of variation for shrivel frequency of 15 populations grown at Yuma, Arizona and Fort Collins, Colorado in 1973. Statistics based on individual plant data grouped across replications and plots to form one sample.

Population	Yuma						Fort Collins					
	n	Mean*	Variance	Range Low	Range High	%	n	Mean*	Variance	Range Low	Range High	%
Parents:												
AB	69	2.7	4.02	1.0	9.0	75.6	92	5.5	3.18	2.0	9.0	32.3
ATL	63	4.4	3.67	1.0	8.0	43.2	97	5.9	4.31	1.0	9.0	35.3
NP	63	3.6	7.26	0.0	9.0	75.0	93	4.1	2.88	1.0	8.0	41.0
F_1's:												
AB/ATL	71	4.3	4.23	1.0	8.0	48.1	91	3.8	3.03	1.0	7.0	46.3
AB/NP	72	2.6	4.35	1.0	8.0	79.5	99	3.2	3.18	1.0	9.0	44.4
ATL/NP	77	2.8	3.29	1.0	7.0	64.7	90	3.8	2.71	1.0	9.0	43.1
BC's:												
2*AB/ATL	70	2.7	3.54	1.0	8.0	69.7	93	5.1	4.67	1.0	9.0	42.2
AB/2*ATL	79	3.7	5.23	1.0	9.0	62.5	95	4.4	4.43	1.0	9.0	48.2
2*AB/NP	75	3.5	6.44	1.0	9.0	72.9	89	5.4	4.35	1.0	9.0	38.7
AB/2*NP	67	3.0	4.61	0.0	9.0	70.8	81	6.2	3.74	2.0	9.0	31.4
2*ATL/NP	73	3.6	5.69	0.0	9.0	66.5	93	5.1	4.80	2.0	9.0	42.8
ATL/2*NP	26	2.2	2.62	0.0	6.0	75.1	86	4.4	4.42	1.0	9.0	48.3
F_2's:												
AB/ATL	150	2.9	4.20	0.0	9.0	70.3	183	4.7	5.18	1.0	9.0	48.1
AB/NP	147	2.9	5.40	0.0	9.0	80.0	184	5.6	4.50	1.0	9.0	37.7
ATL/NP	151	4.0	5.92	0.0	9.0	61.6	181	5.7	4.73	1.0	9.0	38.0

*Measured on a scale of 0 to 9.

Table A12. Analyses of variance of measured traits based on generation means grown at Yuma, Arizona and Fort Collins, Colorado in 1973.

Source	df	Protein						Lysine (% protein)					
		Yuma			Fort Collins			Yuma			Fort Collins		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Reps	3	6.4856			.1173			.0409			.0191		
Genotypes	14	1.9884	4.0	.0004	8.8503	28.2	.0001	.0270	8.9	.0001	.0927	31.4	.0001
Error	42	.4915			.3142			.0030			.0030		
Total	59	1.1515			2.3297			.0106			.0251		

Source	df	Adjusted lysine %						Lysine % (dry weight)					
		Yuma			Fort Collins			Yuma			Fort Collins		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Reps	3	.0388			.0183			.001518			.000932		
Genotypes	14	.0257	8.9	.0001	.0903	31.6	.0001	.003304	11.3	.0001	.001581	6.7	.0001
Error	42	.0029			.0029			.000294			.000234		
Total	59	.0101			.0244			.001070			.000589		

Table A12. (Continued)

Source	df	Shrivel type						Shrivel frequency					
		Yuma			Fort Collins			Yuma			Fort Collins		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Reps	3	.6846			.0151			.9664			2.9473		
Genotypes	14	.0830	1.9	.0584	.0630	4.5	.0002	1.8324	2.4	.0130	2.5880	4.7	.0001
Error	42	.0443			.0141			.7506			.5452		
Total	59	.0860			.0258			1.0183			1.1521		

Source	df	Shrivel index					
		Yuma			Fort Collins		
		MS	F	P	MS	F	P
Reps	3	15.5752			28.6529		
Genotypes	14	18.6319	2.32	.0176	38.5454	5.2	.0001
Error	42	8.0140			7.3571		
Total	59	10.9180			15.8405		

Table A13. Nested analyses of variance to determine between plant variance of protein and lysine as a percent of protein for 15 populations grown at Yuma, Arizona in 1973.

	AB			ATL			NP			AB/ATL F_1		
		MS			MS			MS			MS	
Source	df	Protein	Lysine	df	Protein	Lysine	df	Protein	Lysine	df	Protein	Lysine
Total	68	3.5357	.014063	62	1.6903	.007741	62	3.9182	.013752	70	3.2248	.019713
Rep	3	26.5742	.121631	3	12.9670	.017577	3	30.0117	.148593	3	18.8626	.181390
Between plants	65	2.4724	.009099	59	1.1169	.007241	59	2.5914	.006896	67	2.5246	.012474
CV (%)		8.2	3.3		5.5	3.1		7.8	2.7		8.4	3.9

	AB/NP F_1			ATL/NP F_1			2*AB/ATL			AB/2*ATL		
		MS			MS			MS			MS	
Source	df	Protein	Lysine	df	Protein	Lysine	df	Protein	Lysine	df	Protein	Lysine
Total	71	2.0608	.010253	76	3.4405	.014796	69	5.7359	.029444	78	2.0536	.018228
Rep	3	11.1811	.017958	3	4.4037	.092292	3	45.4464	.295907	3	.8684	.035785
Between plants	68	1.6585	.009913	73	3.4009	.011611	66	3.9308	.017332	75	2.1010	.017525
CV (%)		6.6	3.3		10.1	3.7		11.0	4.5		7.6	4.7

Table A13. (Continued)

Source	2*AB/NP df	2*AB/NP MS Protein	2*AB/NP MS Lysine	AB/2*NP df	AB/2*NP MS Protein	AB/2*NP MS Lysine	2*ATL/NP df	2*ATL/NP MS Protein	2*ATL/NP MS Lysine	ATL/2*NP df	ATL/2*NP MS Protein	ATL/2*NP MS Lysine
Total	74	2.5750	.015604	66	4.0497	.014719	72	4.2400	.011498	25	3.8506	.026851
Rep	3	.3738	.072819	3	8.1359	.071949	3	19.5308	.074393	3	8.4972	.083630
Between plants	71	2.6680	.013187	63	3.8551	.011994	69	3.5751	.008764	22	3.2170	.019108
CV (%)		8.3	3.9		9.9	3.6		10.0	3.3		10.0	4.6

Source	AB/ATL F_2 df	AB/ATL F_2 MS Protein	AB/ATL F_2 MS Lysine	AB/NP F_2 df	AB/NP F_2 MS Protein	AB/NP F_2 MS Lysine	ATL/NP F_2 df	ATL/NP F_2 MS Protein	ATL/NP F_2 MS Lysine
Total	149	2.6254	.013061	146	3.6186	.016233	150	3.6612	.014900
Rep	3	18.0314	.045133	3	4.8195	.007102	3	17.0527	.104491
Row	4	1.4134	.013524	4	3.0434	.007088	4	11.6783	.031385
Between plants	142	2.3341	.012371	139	3.6092	.016694	143	3.1560	.012559
CV (%)		8.1	3.9		9.6	4.3		9.1	3.9

Table A14. Nested analyses of variance to determine between plant variance of protein and lysine as a percent of protein for 15 populations grown at Fort Collins, Colorado in 1973.

Source	AB			ATL			NP			AB/ATL F_1		
	df	MS Protein	MS Lysine	df	MS Protein	MS Lysine	df	MS Protein	MS Lysine	df	MS Protein	MS Lysine
Total	91	3.1812	.024318	96	2.9508	.008990	92	.6544	.005730	90	1.2489	.013611
Rep	3	7.5021	.179887	3	3.0384	.027542	3	2.6868	.040606	3	4.2669	.119152
Between plants	88	3.0339	.019014	93	2.9480	.008391	89	.5859	.004554	87	1.1448	.009971
CV (%)		10.4	4.6		8.0	3.5		4.5	2.2		5.9	10.0

Source	AB/NP F_1			ATL/NP F_1			2*AB/ATL			AB/2*ATL		
	df	MS Protein	MS Lysine	df	MS Protein	MS Lysine	df	MS Protein	MS Lysine	df	MS Protein	MS Lysine
Total	98	.9877	.017711	89	1.3166	.013174	92	4.0148	.019543	94	4.2840	.013406
Rep	3	1.1231	.133951	3	2.0429	.133214	3	2.0514	.061627	3	14.8892	.053240
Between plants	95	.9834	.014040	86	1.2913	.008986	89	4.0809	.018124	91	3.9344	.012093
CV (%)		6.3	3.9		6.5	3.3		11.1	4.7		10.1	4.1

Table A14. (Continued)

Source	2*AB/NP df	2*AB/NP MS Protein	2*AB/NP MS Lysine	AB/2*NP df	AB/2*NP MS Protein	AB/2*NP MS Lysine	2*ATL/NP df	2*ATL/NP MS Protein	2*ATL/NP MS Lysine	ATL/2*NP df	ATL/2*NP MS Protein	ATL/2*NP MS Lysine
Total	88	2.8081	.018805	80	1.4785	.014395	92	3.9814	.014814	85	3.0847	.020576
Rep	3	13.7429	.074713	3	5.5220	.104949	3	14.1473	.082285	3	19.6711	.227714
Between plants	85	2.4222	.016832	77	1.3209	.010867	89	3.6387	.012539	82	2.4779	.012997
CV (%)		9.4	4.3		6.8	3.4		9.7	4.1		8.9	3.9

Source	AB/ATL F_2 df	AB/ATL F_2 MS Protein	AB/ATL F_2 MS Lysine	AB/NP F_2 df	AB/NP F_2 MS Protein	AB/NP F_2 MS Lysine	ATL/NP F_2 df	ATL/NP F_2 MS Protein	ATL/NP F_2 MS Lysine
Total	182	4.6402	.026140	183	2.7594	.018006	180	5.1558	.023981
Rep	3	16.7552	.081350	3	.9406	.031749	3	2.1317	.104019
Plot	4	9.7823	.112080	4	3.5019	.005585	4	8.4678	.069139
Between plants	175	4.3150	.023229	176	2.7735	.018054	173	5.1317	.021549
CV (%)		11.1	5.5		10.1	4.4		12.0	5.1