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Determination of the stability of grain protein production by triticale among nine environments within the southeastern United States

Weyman Parkman Fussell

To the Graduate Council:

I am submitting herewith a dissertation written by Weyman Parkman Fussell entitled "Determination of the stability of grain protein production by triticale among nine environments within the southeastern United States." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Plant, Soil and Environmental Sciences.

Vernon H. Reich, Major Professor

We have read this dissertation and recommend its acceptance:

John H. Reynolds. Fred L. Allen, David W. Brown

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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DETERMINATION OF THE STABILITY OF GRAIN PROTEIN PRODUCTION BY TRITICALE AMONG NINE ENVIRONMENTS WITHIN THE SOUTHEASTERN UNITED STATES

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Weyman Parkman Fussell, Jr.

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ABSTRACT

Twenty-four varieties of hexaploid triticale (Triticosecale Wittmack) were grown in nine environments among five states in the southeastern U.S.A. Seed samples were assayed for percent protein and milligrams protein per hundred seed. Each environment was assigned an index equal to the average of the protein values for all varieties grown in that environment. Each variety was regressed linearly on environmental indices, so as to evaluate stability of seed protein characters over environments. The fit to linear regression was evaluated. Estimates of broad sense heritability for percent protein and milligrams protein per hundred seed were found to be 1% and 11% respectively. Coefficients of variation were 10.1 for percent protein and 12.1 for milligrams protein per hundred seed.

Correlation between seed size and milligrams protein per hundred seed was found to be 0.67; correlation between seed size and percent protein was found to be -0.58. Correlation between percent protein and milligrams protein per hundred seed was 0.18. The correlation between environmental stability (regression coefficients) and protein value was found to be non-significant for both percent protein and milligrams protein per hundred seed. The coefficient of variation was not found to have a significant association with the regression coefficient; therefore, the coefficient of variation should not be used as an indicator of environmental stability. Although protein levels varied among environments, the rankings of individual varieties remained relatively constant among

environments. The results obtained from this study would not preclude the development of a breeding program to enhance protein levels in triticale even though heritability estimates were relatively low.

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I. INTRODUCTION

Direct consumption of cereal grains and food legumes provides, on the average, more than 70% of the dietary calories and protein of all the peoples of Asia, Africa, and Latin America (FAO, 1969; United Nations, 1974). The biological complementarity of cereal and legume protein when eaten in combination is well documented (FAO, 1970). Often, however, obstacles prevent the complementary consumption of cereal and legume foods. These obstacles may result from market limitations affecting the general availability of certain complementary foods, production conditions which are incompatible with crop requirements, or constraints due to cultural alimentary traditions and preference. Cereals will continue to be important sources of dietary protein for those who subsist close to the margin of nutritional adequacy. Increasing attention to the biological quality of the protein is merited in cereal breeding programs if the food needs of the world's hungry are to be met. An increase in either quantity or quality of the grain protein is tantamount to an increase in the effective nutritional yield of the crop without necessarily requiring an actual increase in the crop yield volume. Triticale is one element of the food arsenal, serving as a complement to other cereal grains, and providing a new crop well adapted to a wide variety of conditions and capable of improving the quality of the diets among many of the lesser developed nations.

In solving world food problems, plant breeding plays a key role. However, among plant breeding programs, focus on nutritional

quality has been established infrequently as a priority. There is ample evidence of negative correlations between grain protein quality or quantity and total grain yield. It is difficult to combine the genetic capacities for highest dry matter production and maximum protein storage in one cereal variety. Apparently most of the available genotypes tend to be rich in protein only because of a reduced accumulation of starch in their endosperm (Munck, 1975). In addition, cereals with an increased protein content of their grains generally have lower lysine values in the storage proteins as a consequence of a disproportional increase of the prolamine fraction which is deficient in certain essential amino acids (Munck, 1975).

The drafting of effective strategies for a modern "grain quality" breeding program requires: (1) clear-cut information on the nature and priorities of the various nutritional criteria; (2) sufficiently fast and inexpensive analytical methods for qualitative evaluation; (3) access to sufficient genetic variability. Pursuant to the utilization of a given pool of breeding material and the design of an appropriate breeding program, it can be beneficial to have prior knowledge regarding the heritability of the traits under investigation, correlations between these traits and other characteristics, a representative coefficient of variation, and an indication of the environmental stability of the traits in question. This information may serve as a reference point from which an appropriate breeding program may be designed, based upon the expected variation and an estimation of the rate of progress possible.

This report describes an investigation involving 24 triticale varieties (Triticosecale Wittmack) grown in nine environments. A quantitative evaluation of grain protein was made. The results which are reported herein provide estimates of the following: (1) heritability for absolute protein per seed in terms of milligrams protein per hundred seed; (2) heritability for percent protein; (3) correlations between seed protein and seed weight; (4) coefficients of variation for seed protein analysis; (5) an evaluation of the stability of protein quantity over a variety of environments. Reported also are the results of an unsuccessful experimental attempt to evaluate the mode of interaction of the wheat and rye genomes with regard to seed protein characters.

It is hoped that the results reported herein may be of value in the planning and execution of a triticale breeding program which seeks to improve the protein quality of this food source.

II. REVIEW OF LITERATURE

Triticale (Triticosecale Wittmack) is the common name of the plant genus produced by crossing wheat (genus Triticum) with rye (genus Secale). Triticosecale, proposed by Baum (1971), is the generic name for triticale derived from F_1 hybrids in which Triticum is the female parent. Secalotriticum, proposed by Rosenstiel and Mittelstenscheid (1943) and Tschermak (1938), is reserved for triticale derived from F_1 hybrids in which Secale is the female parent.

Successful attempts to artifically produce a hybrid between wheat and rye were first reported in 1875 (Wilson) in a presentation to the Botanical Society of Edinburgh. Since that time numerous attempts have been made to combine the productivity and baking qualities of Triticum with the vigor and hardiness of Secale. However, it was not until the 1930's that plant breeders first evaluated triticale as a potentially new field crop (Muntzing, 1939). The early triticale development programs utilized the octoploid forms (2n=8x=56) in which the wheat parent was hexaploid T. aestivum ("bread" wheat). Subsequently, work with hexaploid triticale (2n=6x=42) indicated that these were superior in meiotic stability and fertility relative to octoploids (Sanchez-Monge and Tijo, 1954; Sanchez-Monge, 1956, 1958).

Early work in triticale development was initiated during the 1930's in Sweden, Germany, and the United States, and during the 1940's in Russia. The first large scale triticale breeding program

on the North American continent was initiated in 1954, at the University of Manitoba, Winnipeg, Canada.

Depending upon the breeder and the particular goals, five reasonably distinct approaches to the development of triticale have been utilized:

(1) primary octoploid forms (Muntzing, 1963);

(2) secondary forms derived from octoploid x hexaploid crosses (Pissarev, 1966; Kiss, 1966);

(3) hexaploid triticale x hexaploid wheat (Nakajima and Zennyozi, 1966);

(4) triple hybrids involving hexaploid wheat, tetraploid wheat, and rye (Muntzing, 1935; Shulydin, 1972);

(5) hexaploid triticale x hexaploid triticale (Jenkins, 1966).

The term "primary triticale" is used to designate those strains which are the immediate products of chromosome doubling following a wheat x rye cross. The term "secondary triticale" describes those triticales that are derived from crosses between octoploid and hexaploid forms, such as in approach (2) above. Secondary triticales are usually hexaploid, but also secondary octoploids can be obtained. Secondary triticales may possess either Triticum aestivum L. em. Thell cytoplasm or Triticum durum Desf. cytoplasm, depending on the direction of the cross. Approach (3) is utilized to produce "substitutional triticale." In this case, various chromosomes from the rye (Secale) complement may be replaced by chromosomes of the D-genome out of T. aestivum. "Triple hybrids" are those which are derived from three species (hexaploid wheat, tetraploid wheat, diploid rye) by

direct crosses among themselves. "Recombined triticales" are those resulting from intercrosses among lines belonging to the same chromosome level, such as would be obtained by approach (5) above.

The chromosomal control of endosperm proteins in wheat and rye has been studied extensively (Shepherd, 1968; Wrigley, 1972; Jagannath and Bhatia, 1972). The protein contents of wheat and rye have been shown to vary widely among different varieties grown under different environmental conditions (Kent-Jones and Amos, 1967). The nutritional quality of cereal protein is dependent upon its biochemical composition. This is conditioned by genetic background which in turn interacts with the environment in which the plant is grown, including the agronomic practices by which it is produced. This interaction of genetic and environmental factors often serves to complicate the predictability of performance that is characteristic of a given variety. Since conclusions about inheritance are inferred from phenotypic observations, appropriate interpretations depend on understanding the nature and the causes of phenotypic variation. Likewise, predictions as to performance under diverse environmental conditions demands an understanding of both qualitative and quantitive nature of the effects of genetic and environmental interaction.

In an effort to deal with the problem of quantitatively measuring adaptability itself, Finlay and Wilkinson (1963) used the regression of the yield of a particular variety on the grand mean yield obtained at each environment for an entire set of varieties. The regression coefficients were then used to draw conclusions regarding the general stability of a variety under varying environmental

conditions. Eberhart and Russell (1966) developed a similar technique. However, their method included the use of residual deviations from the regression as a way to measure the unpredictable variations which occur in response to the environment. Eberhart and Russell suggested that an appropriate evaluation of genotypes would enable the breeder to identify the more stable lines. Subsequently, the more stable genotypes could be carried forth for the final stages of improvement or testing in a breeding program where stability of performance over a range of environments is a program goal.

A primary objective of quantitative genetic analysis is the estimation of the magnitude of genetic variance as it pertains to predicting the rate of genetic improvement in selection programs. It might be argued that no very exact information about the relative size of genetic variance is really needed since, regardless of its magnitude, the breeder must nevertheless go ahead with the program, and that what will actually be achieved would not be changed much anyway. Comstock and Moll (1963) have demonstrated statistically that the effect of a large GxE interaction is to reduce progress in selection programs, and have pointed out several reasons that general acceptance of an indifferent point of view could be counterproductive. First of all, they concluded that overestimation of the amount of genetic variance present may lead to investment of time and resources not justified by the real potential for improvement represented by the genetic stocks employed. Also, the selection of the optimum breeding strategy may vary depending upon the magnitude of the variance. Furthermore, they reasoned that there is the possibility

that a sound breeding program may be abandoned prematurely or for the wrong reasons because of results that are disappointing relative to expectations based upon erroneous estimates of genetic variance. However, the argument is not that the breeder should necessarily obtain estimates of genetic parameters for every population employed in a breeding program. The cost of exhaustive estimates of these parameters suggests that a limited number of good estimates be obtained and utilized for inference concerning generally similar materials.

III. MATERIALS AND METHODS

Seed Protein Characters

A collection of 24 winter hexaploid triticale varieties (Triticosecale) were grown in nine locations among five states in the southeastern United States. These varieties were grown as a part of the Regional Uniform Triticale Yield Nursery. The entries were planted in randomized complete block layouts in the fall of 1979 and harvested in the summer of 1980. Each location represented a separate environment without requirement of uniform cultural practices. A summary of varieties and locations is given in Table 1. The varieties and environments represented in this study are not the objects of examination per se, but rather examples which are employed in order that general inferences may be made regarding similar material.

Unground whole seed subsamples of approximately 0.2000 gram were weighed from each replicate; each weight was recorded exactly. The hundred seed weight was also recorded.

Each subsample was chemically digested using concentrated H_2SO_4 and 30% H_2O_2, based on the procedure of Linder and Harley (1942) modified by the addition of H_2O_2 as suggested by Miller and Miller (1948). The laboratory procedure for nitrogen digestion is included in the Appendix. Nitrogen analysis was performed on an Auto Analyzer by the Plant and Soil Science Department, The University of Tennessee, Knoxville (Thomas et al., 1967). Laboratory results

Table 1. Triticale varieties, corresponding entry numbers, locations at which they were grown in 1979 and 1980, and environmental indices corresponding to each location.

		Location								
		Huntsville, AL	Tallassee, AL	Experiment, GA	Tifton, GA	Clemson, SC	Marianna, AK	Rohwer, AK	Keiser, AK	Knoxville, TN
Variety	Entry Number									
AM 4105	1	X	X	X	X	X	X	X	X	X
ARK 2005	2		X	X	X	X	X	X	X	X
ARK 2014	3	X	X	X	X	X	X	X	X	X
ARK 2092	4		X	X	X	X	X	X	X	X
OK 77842	5	X	X	X	X	X		X	X	X
AM 3948	6	X	X	X	X	X	X	X	X	X
6TA 131A	7	X	X	X	X	X	X	X	X	X
OK 77803	8	X	X	X	X	X	X	X	X	X
AM 4109	9	X	X	X	X	X	X	X	X	X
AM 3235	10	X	X	X	X	X	X	X	X	X
6TA 522	11	X	X	X	X	X	X	X	X	X
AM 4142	12	X	X	X	X	X	X	X	X	X
OK 77802	13	X	X	X	X	X	X	X	X	X
AM 2873	14	X	X	X	X	X	X	X	X	X
AM 4115	15	X	X	X	X	X	X	X	X	X
AM 4108	16	X	X	X	X	X	X	X	X	X
6TA 313	17	X	X	X	X	X	X	X	X	X
OK 77824	18	X	X	X	X	X	X	X	X	X
6TA 876	19	X	X	X	X	X	X	X	X	X
OK 78828	20	X	X				X	X	X	
OK 77801	21	X	X				X	X	X	
OK 77843	22	X	X				X	X	X	
OK 77826	23	X	X				X	X	X	
ARK 2301	24	X	X				X	X	X	
Environmental Indices										
Percent protein		10.3	16.4	11.5	11.6	11.5	9.6	9.3	11.7	12.6
Milligrams protein per hundred seed		374.3	443.7	440.5	522.8	345.7	452.7	373.9	497.3	335.0

were obtained in parts per million (ppm) nitrogen. Conversions were made to percent protein and also milligrams protein per hundred seed (MPHS). A conversion factor of 6.25 was used to convert percent nitrogen to percent protein.

Statistical analyses were performed on the data using an electronic computer and Statistical Analysis System (SAS) 79 programming. Table 2 shows the analysis of variance model, after Eberthart and Russell (1966). Milligrams protein per hundred seed (MPHS) and percent protein were each regressed on their respective environmental indices. Each environment was assigned an index equal to the average of the protein values for all varieties grown in that environment (Table 1). This produced two sets of environmental indices: one for MPHS and one for percent protein. As such, the index is taken as a composite measure of all environmental factors which affect the protein character at a given location. From the regression relationships, the regression coefficients were determined for each variety and used as a measure of varietal stability over the range of environmental conditions.

Estimates of broad sense heritability were made for MPHS and percent protein. Coefficients of variation were calculated from analysis of variance estimates. Coefficients of variation (CV) were also calculated for each variety from regressional relations as given by

$$CV = 100 \frac{(MS_{\text{deviation from regression}})}{\overline{X}_i} .$$

Table 2. Generalized analysis of variance for estimation of stability parameters (after Eberhart and Russell, 1966).

Source	df		Sums of squares
Total	nv-1		$\sum_i \sum_j Y_{ij}^2 - CT$
Varieties (V)	v-1		$1/n\ \Sigma Y_{i.}^2 - CT$
Environments (E)	n-1	v(n-1)	$\sum_i \sum_j Y_{ij}^2 - \Sigma \frac{Y_{i.}^2}{n}$
V x E	(v-1)(n-1)		
E (linear)	1		$1/v\ \left(\sum_j Y_{.j} I_j\right)^2 \Big/ \sum_j I_j^2$
V x E (linear)	v-1		$\sum_i \left[\left(\sum_j Y_{ij} I_j\right)^2 \Big/ \sum_j I_j^2 \right] - E(\text{linear})ss$
pooled deviations	v(n-2)		$\sum_i \sum_j \delta_{ij}^2$
variety 1	n-2		$\left[\sum_j Y_{ij}^2 - (Y_{i.})^2 \right] - (\Sigma Y_{ij} I_j)^2 \Big/ \Sigma I_j^2$
	.		.
	.		.
	.		.
variety 24	n-2		$\left[\sum_j Y_{24j}^2 - \left(\frac{Y_{24.}}{n}\right)^2 \right] - \left(\sum_j Y_{24j} I_j \right)^2 \Big/ \sum_j I_j^2 = \sum_j \delta_{24j}^2$
Pooled error	n(r-1)(v-1)		

Correlations were calculated between protein characters and seed size, and between regression coefficients and mean protein values.

Attempt to Produce F_1 Wheat x Rye Plants

Three varieties of Triticum durum Desf. representing high, medium, and low seed protein levels were crossed with three winter rye varieties (Secale cereale L.) also representing high, medium, and low seed protein levels. These crosses were made in all possible combinations, without reciprocals, giving a total of nine cross combinations. The plants were grown in pots under greenhouse conditions. The wheat florets were emasculated by hand and the glumes clipped so as to expose the stigmas. T. durum Desf. represented the female parent in all crosses. Emasculated wheat spikes and rye spikes with dehiscing anthers were bagged together using bags made from dialysis tubing. Crossing was accomplished by natural pollenshed of the rye upon the emasculated wheat florets. The seeds were harvested at plant senescence and tested for respiration with tetrazolium.

IV. RESULTS AND DISCUSSION

Seed protein was analyzed among the 24 varieties over nine environments. Protein values were obtained on the basis of both percent protein and milligrams protein per hundred seed (MPHS). Correlation coefficients were calculated among variables for percent protein and MPHS.

Results are also reported for an unsuccessful attempt to produce F_1 wheat x rye plants.

Percent Protein

Analysis of variance showed the differences among varieties and differences among environments to be significant (Table 3). The coefficient of variation (CV) was 10.1%.

Each variety was linearly regressed on the environmental indices (I_i; where i = 1, 2, ..., 9, corresponding to the nine environments). Sums of squares due to regression and due to deviations from regression ($\hat{\delta}^2$), and mean square (MS) due to deviations from regression were tabulated for each variety (Table 4). Mean squares for deviations from regression indicated good fit to linear regression among the varieties with two exceptions. Varieties 6TA 876 and OK 77801 had deviations from regression which were statistically significant.

An estimate of the stability parameter σ_d^2 (s_d^2) was calculated for each variety from the following relationship:

$$s^2_{d_v} = \left[\frac{\hat{\delta}^2_v}{(n-2)}\right] - \frac{s^2_e}{n}$$

Table 3. Pertinent components from analyses of variance for percent protein and milligrams protein per hundred seed (MPHS), and the respective coefficients of variation (CV).

Source	df	Mean square	
		% protein	MPHS
Varieties (V)	23	3.2**	18,564.3**
Environments (E)	8	241.7**	147,112.0**
V x E	161	2.1*	4,827.8**
Replications within E	6	3.7*	6,017.1
Residual	121	1.4	5,540.6
Total	319		
CV (% protein) = 10.1%			
CV (MPHS) = 12.1%			

*indicates significance at $P \leq 0.05$.

**indicates significance at $P \leq 0.01$.

Table 4. Sums of squares (SS) due to regression, degrees of freedom (df) for deviations from regression, SS due to deviations from regression ($\hat{\delta}^2$), and mean squares (MS) of deviations from regression for linear regression of individual varieties on environmental indices for percent protein for 24 triticale varieties.

Variety	SS due to regression	df	$\hat{\delta}^2$	MS
AM 4105	72.21	13	19.87	1.53
ARK 2005	50.71	11	20.88	1.90
ARK 2014	133.57	13	17.61	1.35
ARK 2092	104.82	11	14.42	1.31
OK 77842	103.90	12	24.85	2.07
AM 3948	97.58	13	37.20	2.86
6TA 131A	70.87	13	25.49	1.96
OK 77803	104.43	13	43.37	3.34
AM 4109	81.09	13	10.89	0.84
AM 3235	30.69	13	7.68	0.59
6TA 522	30.37	13	33.35	2.57
AM 4142	66.00	13	20.32	1.56
OK 77802	80.71	13	17.14	1.32
AM 2873	60.33	13	28.12	2.16
AM 4115	113.11	13	25.00	1.92
AM 4108	63.00	13	24.57	1.89
6TA 313	89.82	13	24.18	1.86
OK 77824	86.13	13	5.95	0.46
6TA 876	94.20	13	46.24	3.56*
OK 78828	140.88	6	9.61	1.60
OK 77801	60.97	6	73.66	12.28**
OK 77843	57.73	6	13.69	2.28
OK 77826	92.27	6	2.63	0.44
ARK 2301	106.34	6	1.82	0.30

*indicates value is significantly different from zero at $P \leq 0.05$.

**indicates value is significantly different from zero at $P \leq 0.01$.

where v = 1, 2, ... 24; corresponding to the 24 varieties

n = number of observations involved in the deviation sum of squares for the variety under examination

(n-2) = degrees of freedom for "deviations from regression" for the variety under examination

s_e^2 = the pooled error mean square (derived from the sum of the deviation sums of squares for all varieties).

For each variety, Table 5 gives the values of s_d^2, the linear regression coefficient (b), and the mean percent protein ($\overline{X}$). The utility of these data is discussed in the following paragraphs.

The regression lines for varieties representative of high, medium, and low b-values are shown in Figure 1. These graphs illustrate the variation among the permutations of b-value and mean protein value combinations exhibited by the varieties under examination.

The regression coefficient (b) is an indicator of the amount of G x E interaction for a given variety over the array of environments. If the objective is to select varieties which provide a stable and predictable performance in the face of uncertain environmental conditions, then a variety with a regression coefficient of zero and a low deviation from regression would tend to fulfill that objective. The ideal variety, it may be argued, is one which combines stability with exceptional mean performance. In practice, however, alternative choices usually require a trade-off between mean value and stability. The variety with the highest mean performance is not necessarily the variety with the regression coefficient which most nearly approaches zero. For example, variety 6TA 131A possessed

Table 5. Mean percent protein ($\bar{X}$), coefficient of variation (CV), and estimates of stability parameters (b and s_d^2) for percent protein for 24 triticale varieties.

Variety	s_d^2	b	CV	$\bar{X}$
AM 4105	1.43	0.96	10.2	12.05
ARK 2005	1.80	0.85	10.7	12.86
ARK 2014	1.25	1.30	9.2	12.58
ARK 2092	1.21	1.22	9.3	12.36
OK 77842	1.97	1.20	11.5	12.47
AM 3948	2.76	1.11	13.4	12.65
6TA 131A	1.86	0.95	10.6	13.14
OK 77803	3.24	1.15	15.5	11.79
AM 4109	0.74	1.02	7.8	11.71
AM 3235	0.49	0.63	6.0	12.85
6TA 522	2.47	0.63	12.6	12.65
AM 4142	1.46	0.92	10.1	12.39
OK 77802	1.22	1.01	9.7	11.84
AM 2873	2.06	0.88	12.8	11.51
AM 4115	1.82	1.20	11.5	12.03
AM 4108	1.79	0.90	11.7	11.74
6TA 313	1.76	1.07	11.4	11.94
OK 77824	0.36	1.05	5.7	11.91
6TA 876	3.46	1.09	15.4	12.20
OK 78828	9.41	1.37	10.4	12.14
OK 77801	12.08	0.90	12.1	12.04
OK 77843	2.08	0.88	12.3	12.26
OK 77826	0.24	1.11	5.5	11.94
ARK 2301	0.10	1.19	4.6	11.96
				$\bar{\bar{X}}$ = 12.21

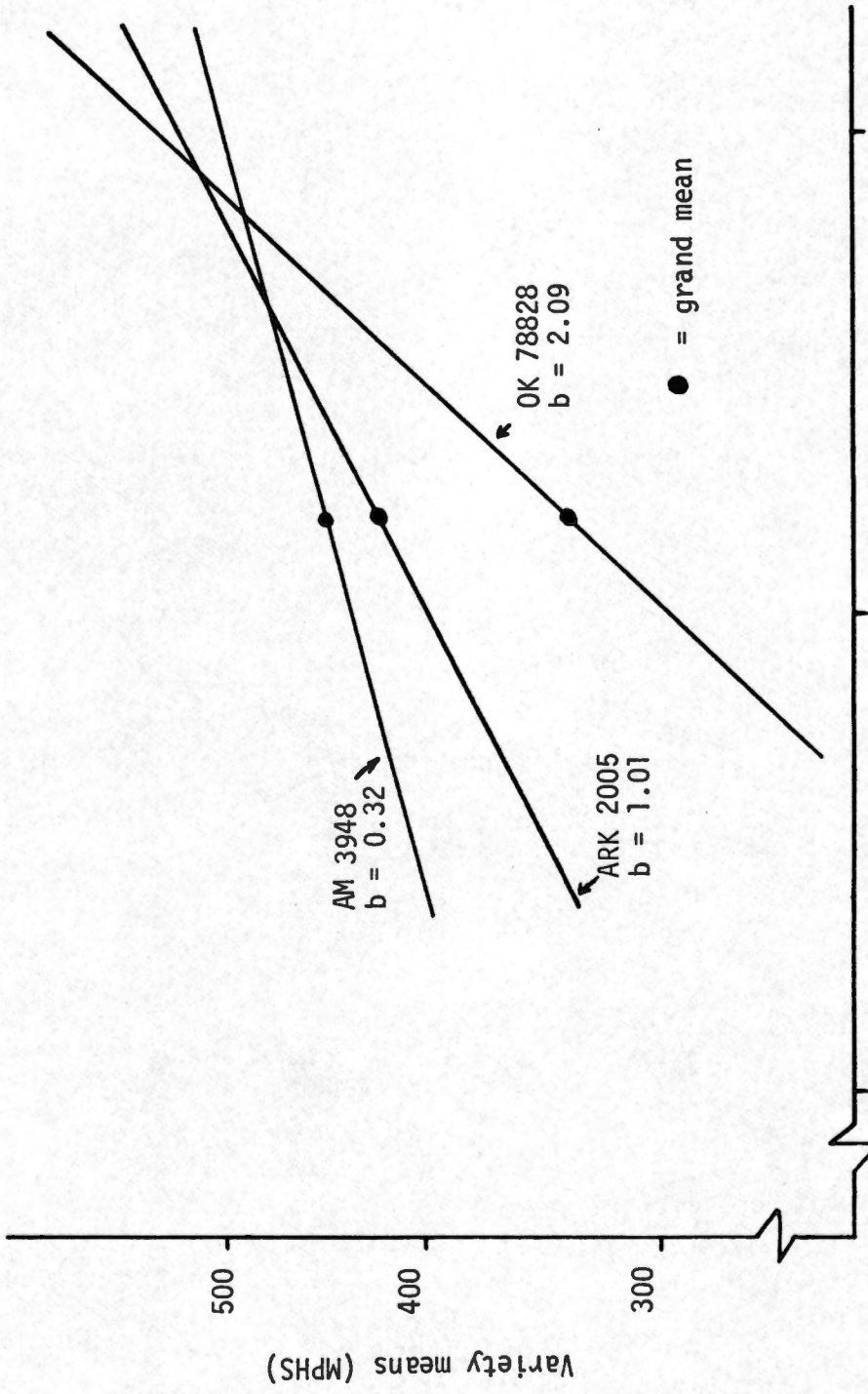

Figure 1. Representative relationships for regression of variety on environmental indices for percent protein.

the highest mean percent protein but was observed to have a relatively high b-value. This leads to the question as to whether there is anything in the inherent nature of the relationship between variety mean and the regression coefficient which would obstruct the simultaneous maximization of mean and stability for percent seed protein in a single variety. To address this question the correlation coefficient was calculated between the regression coefficients (b_v) and the corresponding means ($\bar{X}_v$) for all varieties. The correlation coefficient was found to not differ significantly from zero ($P > 0.05$). This suggests that there is no meaningful correlation between these two variables and, consequently, no reason to assume a priori that a program which seeks to simultaneously maximize mean and stability would represent a conflict in purposes.

If linear regression is to be used to evaluate the stability of varieties, it is necessary to be assured that the regression does in fact satisfactorily represent the relationship between the regressed variables. An estimate of the stability parameter σ_d^2 (s_d^2, Table 5) for each variety can be used to evaluate the fit to linear regression. Alternatively, the sums of squares for deviations from regression ($\hat{\delta}^2$, Table 6) can be tested for significance ($H_o: \hat{\delta}^2 = 0$) and these values used as a measure of fit of the regression. On the other hand, the calculation of s_d^2 attempts to remove from the deviations the part of the variation which is unexplained by linear effects, leaving a value which is the result of higher order (non-linear) relationships. If this value is large, then there is an indication that non-linear relationships account for proportionately more of the variation, an

indication that linear regression provides an accordingly less accurate prediction of the variety performance. For this reason s_d^2 is considered a better evaluation of the adequacy of the linear regression that does $\hat{\delta}^2$. Ideally, a single parameter that includes mean, regression coefficient, and deviation from regression should be used as a measure of stability. However, it is not possible with the existing knowledge to determine what weights should be assigned to each component.

In the case of MPHS there was no significant deviation from linear regression for any variety (Table 6); thus, one may assume that non-linear deviations from linear regression as measured by s_d^2 (Table 7) are also non-significant. On the other hand, in the case of percent protein, varieties 6TA 876 and OK 77801 are found to deviate significantly from linear regression and, therefore, are not adequately described by such a representation (Table 4). Using s_d^2 from Table 5, it is revealed that 97% $\left(\frac{s_d^2}{MS} = \frac{3.46}{3.56}\right)$ and 98% $\left(\frac{s_d^2}{MS} = \frac{12.08}{12.28}\right)$ of the deviations from linear regression for 6TA 876 and OK 77801 respectively are due to higher order regressional relationships. Thus, higher order mathematical descriptions of the relationship between percent protein and environmental influence must be sought for these varieties under the given range of experimental environments.

The coefficient of variation (CV) may be used as a measure of fit to linear regression for a given variety (Table 5). Correlation between s_d and CV was found to be 0.74 ($P < 0.01$). The high

Table 7. Mean milligrams protein per hundred seed ($\overline{X}$), coefficients of variation (CV), and estimates of stability parameters (b and s_d^2) for milligrams protein per hundred seed for 24 triticale varieties.

Variety	s_d^2	b	CV	$\overline{X}$
			%	mg
AM 4105	1611	0.76	11.1	399.1
ARK 2005	3251	1.01	13.9	434.4
ARK 2014	4924	0.88	11.8	423.7
ARK 2092	3956	1.36	15.0	440.0
OK 77842	4623	0.61	16.3	434.0
AM 3948	5305	0.32	15.9	473.6
6TA 131A	2401	1.40	9.7	544.9
OK 77803	6585	1.24	19.7	423.8
AM 4109	2366	0.81	13.2	395.8
AM 3235	1760	0.36	12.0	384.1
6TA 522	4907	0.81	17.8	408.2
AM 4142	2553	0.88	12.0	449.4
OK 77802	3377	0.51	14.4	424.9
AM 2873	5658	0.98	17.4	444.8
AM 4115	4137	0.66	14.7	456.1
AM 4108	2816	1.41	11.9	474.0
6TA 313	1963	0.50	12.2	395.6
OK 77824	1200	0.66	9.6	411.9
6TA 876	3881	0.43	18.2	359.0
OK 78828	1921	2.09	14.4	354.7
OK 77801	814	1.44	11.5	338.1
OK 77843	3364	0.94	18.4	345.6
OK 77826	432	1.24	10.6	316.8
ARK 2301	1623	1.41	14.0	343.6
				$\overline{\overline{X}}$ = 418.9

correlation is not surprising since both s_d and CV are a function of the mean square due to deviations from regression. For a given variety:

$$CV = 100 \quad \frac{(MS_{\text{dev. from regression}})}{\bar{X}_i}$$

and

$$s_d^2 = (MS_{\text{dev. from regression}}) - \frac{s_e^2}{n}$$

The coefficient of variation was not found to have a significant ($P > 0.05$) association with the regression coefficient (b) and, therefore, the CV should not be used as an indicator of environmental stability.

While regression may provide an adequate picture of varietal response over the range of experimental environments, any extrapolation beyond this range must be done under the assumption that the observed relationship persists into the extrapolated region. Such an assumption may prove to be unjustifiable. Thus, when planning a test of environmental stability, thought should be given to the types and range of environments which will be utilized so as to encompass environments which will be representative of the projected deployment areas.

The broad sense heritability (H^2) was calculated for percent protein. This value was found to be 0.01, as based on the relationship

$$H^2 = \frac{\text{total genetic variance}}{\text{total phenotypic variance}} = \frac{\sigma_v^2}{\sigma_v^2 + \sigma_e^2 + \sigma_{vxe}^2 + \sigma_r^2}$$

where

σ_v^2 = variance among varieties

σ_e^2 = variance among environments

σ_{vxe}^2 = variance due to variety x environment interactions

σ_r^2 = variance due to factors not explained by the other variance terms

The heritability value of 0.01 (1.0%) is low. This indicates that a very small proportion of the variation in percent protein among the varieties in the experimental population is due to genetic variation. That is to say, variation in percent protein is more strongly affected by variations due to environmental influence than by variations in the genetic backgrounds among the varieties. A population with low genetic variability provides a generally undesirable base for a breeding program. The environmental influence on the level of protein in wheat is known to be large. It has been shown that the protein content of hard wheat varieties may vary from 8% to 18% as a function of environment (Johnson et al., 1968). Thus, the term "high protein" is relative and does not imply a fixed level, but rather implies a high level relative to other varieties grown in the same environment. Environmental factors have often been observed to alter the endosperm protein character of hard winter wheats when grown in the generally more warm and humid climates characteristic of the soft winter wheat regions. In such cases the hard wheat is observed to exhibit the endosperm protein character of soft wheats and the trait commonly

referred to as "yellow berry." It would not be unreasonable to expect that the strong influence of environment on protein which is typical of wheat would also be prevalent among the triticale progeny.

Milligrams Protein Per Hundred Seed (MPHS)

The analysis of variance showed the differences among varieties and differences among environments to be significant (Table 3, page 15). The coefficient of variation was 12.1%.

Sums of squares due to deviations from regression ($\hat{\delta}^2$, Table 6) were tabulated for each variety and used to calculate an estimate of the stability parameter σ_d^2 (s_d^2) following the same procedure as was used for corresponding values for percent protein. For each variety, Table 7 gives the values of s_d^2, the linear regression coefficient (b), the mean MPHS ($\overline{X}$), and coefficients of variation (CV). While heritability values for percent protein and MPHS are both low in absolute terms and suggest the need for a breeding scheme tailored for a low heritability situation, selection for MPHS may be expected to proceed more rapidly than for percent protein from the population under examination.

Correlations Among Protein Values

Table 8 gives correlation coefficients among percent protein, MPHS, the respective environmental indices, and seed weight. Correlation between MPHS and seed weight is 0.67, indicating a relatively close relationship between absolute protein and seed size. It should not surprise one to discover that larger seeds tend to contain larger

Table 8. Correlation coefficients among characters.

Character	% protein	MPHS	Seed weight	Index (MPHS)	Index (% protein)
% protein	1	0.18**	-0.58**	-0.04^{ns}	0.87**
MPHS		1	0.67**	0.67**	-0.03^{ns}
Seed weight			1	0.57**	-0.64**
Index (MPHS)				1	-0.09^{ns}

**indicates that correlation coefficient is significantly different from zero at $P \leq 0.01$.

^{ns}indicates that correlation coefficient is not significantly different from zero at $P \leq 0.05$.

amounts of protein. It should be considered that selection for higher MPHS alone may essentially result in selection for larger seed and lead to no genuine improvement in nutritional quality per volume of grain. Breeding for higher MPHS may result in more protein per hectare, but will not necessarily result in more protein per unit of grain consumed. Thus, it seems that if meaningful improvement is to be made in nutritional quality in terms of protein quantity, the improvement must be reflected as an increase in percent protein per volume or weight of grain or flour.

There is a fairly strong negative correlation (-0.58) between seed size and percent protein. This follows logically since smaller seed are usually the consequence of smaller endosperm, leaving the high protein embryo to account for a larger fraction of the total seed mass. If selection for higher percent protein leads to small seed, then the breeder is faced with the additional task of selecting for greater seed number per plant in order to avoid suffering a reduction in grain yield per hectare. According to Atale and Joshi (1979), following a study involving 30 triticale varieties, grain yield per plant in grams is highly correlated with the number of grains per spike ($r = 0.66$) and the number of spikes (tillers) per plant ($r = 0.81$).

If the objective were to increase percent protein and maintain grain yield per hectare, the alternatives may involve the selection for high percent protein in conjunction with:

(1) selection for large seed; or

(2) selection for more seed per plant through

a. more seed per spike; or

b. more spikes per plant.

In evaluation of the alternatives, one important consideration would be the environmental stability of the trait that is to be concomitant with percent protein since this would translate into stability of yield.

The high correlations between percent protein and index (%protein), and between MPHS and Index (MPHS) are to be expected since the indices are a function of the respective protein values. The more closely the protein values among the varieties are clustered about the mean protein value, then the higher the correlation will be between the indices and the various protein values.

The correlation between percent protein and MPHS is low (0.18). This suggests that these characters are reasonably independent, and that association between them is independent of seed size.

Figure 2 depicts three representative regression relationships for MPHS and environmental index. These graphs illustrate the variation among the various combinations of stability and mean value within the varieties under examination. The variance and range among b-values were found to be greater for MPHS than for percent protein. The mean b-values for percent protein and MPHS were similar, 1.02 and 0.95 respectively. However, b-values ranged from a low of 0.63 to a high of 1.37 for percent protein, while the range for MPHS was 0.36 to 2.09. As was the case for percent protein, the correlation between the regression coefficients and the means was calculated and found not to be significantly different from zero ($P > 0.05$).

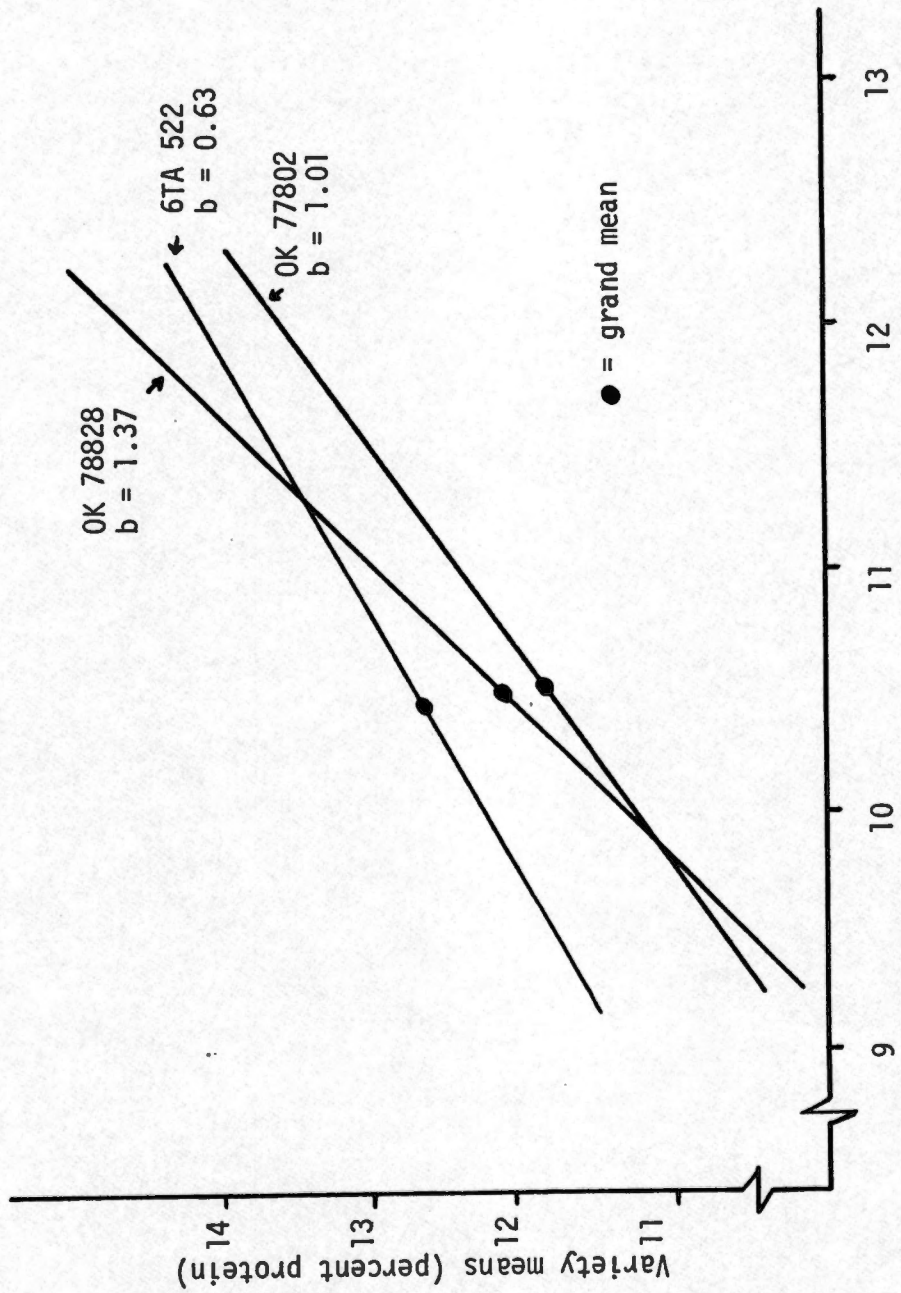

Figure 2. Representative relationships for regression of variety means on environmental indices for milligrams protein per hundred seed (MPHS).

This suggests that there is no close connection between MPHS and environmental stability for this trait and suggests that there should be no inherent conflict in a breeding program which seeks to maximize both protein quality and environmental stability of this character. Deviations from regression (Table 6, page 21) tested to be non-significant for all varieties, indicating good fit to linear regression in all cases.

The correlation between the coefficients of variation and s_d^2 was 0.75 ($P < 0.01$), reflecting the close association between these two statistics with regard to the fit of the linear regression model.

Broad sense heritability was found to be relatively low at 11.0%. However, this value for MPHS is notably higher than for percent protein, indicating relatively greater genetic variation with regard to absolute protein quantity.

Plant breeding is a relatively efficient way to improve the nutritional quality of cereal grains. A new improved variety produces better quality with little or no additional expenditures for management inputs or food additives. It appears that breeding for quality can only be successful when conducted as part of an overall program in which yield factors have high priority since it has yet to be decided who will pay the farmer for a nutritionally superior product. While the available information indicates that there should be no conflict per se in objectives of a breeding program which seeks to maximize mean seed protein and environmental stability of seed protein simultaneously, it is evident that such a program would be faced with the additional task of maximizing and stabilizing yield in light

of the correlations between protein quantity and seed size. The complexity of such a challenge lends appeal to the idea of improving protein value through the relatively straightforward task of optimizing the amino acid balance by increasing the amount of lysine present in the endosperm.

A better understanding of the nature of the interactions among the wheat and rye genes controlling protein quantity and quality as they combine in the triticale genotype would be of value in developing grain of superior nutritional quality.

In addition to the obvious requirement of maintaining the energy level and the yield while increasing the protein value of the grain, attention should be given to the need for improving the nutritive value and digestibility of the proteins. Attention should be paid to the effects of local practices upon the digestibility, nutritive value, and baking properties of the final product as grain for human consumption is normally processed and cooked.

Under the conditions of a carefully controlled environment, it may be possible to uncover relationships between protein value and various environmental components. Experimental control in the variation of such factors as fertility level, moisture supply, plant density, or planting date could provide the basis for environmental indices capable of more clearly defining the relationship between environment and grain quality and stability.

Attempt to Produce F_1 Wheat x Rye Plants

Nine cross-combinations were represented by the intermating of the three wheat varieties with the three rye varieties. A total of 1920 florets was pollinated with an average of six florets per spike. This produced a total of 96 seeds among the nine cross-combinations. The number of seeds produced per parental combination ranged from a minimum of seven to a maximum of 12.

The seed were harvested after the plants appeared to have completed senescence. All seeds were severely shrunken. Respiration was tested with tetrazolium. None of the seeds was found to show signs of respiration; therefore, no F_1 hybrids were produced.

Embryos from wheat x rye crosses have a very low rate of viability. For maximum survival the embryos should be excised from the developing seed shortly after fertilization (on the order of 7 to 12 days), germinated and cultured on appropriate media under sterile laboratory conditions in a controlled environment. Following the establishment of the young plant, a colchicine treatment should be applied in order to accomplish chromosome doubling (Beatty et al., 1976; Rupert, 1980).

Embryo excision and culture were not performed due to limitations on expertise and facilities. Embryo culture is widely accepted as the preferred method for F_1 production of wheat x rye crosses due to the relatively high rate of success as compared to natural seed development and germination. Success in producing viable mature seed under greenhouse conditions can be enhanced with proper control of

ambient temperature and humidity. Appropriate facilities for this purpose were not readily available.

V. SUMMARY

Twenty-four varieties of hexaploid triticale were grown in nine environments among five states in the southeastern United States. Results showed broad sense heritability for seed protein in terms of milligrams protein per hundred seed (MPHS) and for percent protein to be low in both cases, 11% and 1% respectively. These values indicate that variation in MPHS and percent protein is more strongly affected by variations among environments than by variations in the genetic backgrounds among the varieties.

Protein characters were regressed on environmental indices, revealing variation among the varieties with regard to environmental stability as measured by the regression coefficient. The correlation between stability (regression coefficients) and protein value was found to be non-significant for both percent protein and milligrams protein per hundred seed. A fairly strong positive correlation was found between seed size and milligrams protein per hundred seed (0.67). A negative correlation was found to exist between seed size and percent protein (-0.58). The coefficient of variation (CV) was 10.1% for percent protein and 12.1% for milligrams protein per hundred seed for the experimental conditions encountered. The coefficient of variation was not found to have a significant ($P < 0.05$) association with the regression coefficient (b) and, therefore, the CV should not be used as an indicator of environmental stability.

Variety AM 3948 displayed both the lowest coefficient of regression (0.32) and the third highest mean protein value for MPHS.

For percent protein the variety AM 3235 showed the lowest coefficient of regression (0.63) among the varieties tested, and a relatively high mean percent protein (12.85%).

Deviations from regression were calculated for each variety in order to evaluate the extent to which linear regression gave a suitable representation of the relationships under investigation. Deviations from linear regression were found to be insignificant for all varieties in the case of milligrams protein per hundred seed. Two varieties showed significant deviations from linear regression for percent protein.

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APPENDIX

NITROGEN DIGESTION PROCEDURE

1. Weigh approximately 0.2000 gram of whole grain material into 125 ml. Erlenmeyer flask.

2. Add 10 ml. concentrated H_2SO_4 and let pre-digest overnight. Place on cool hotplate.

3. Heat at high temperature (approximately 220°C) until volume is reduced by 50% (about 2 1/2 hours).

4. Set off hotplate and let cool.

5. When cool enough to hold in palm of hand, add 20 ml. of 30% H_2O_2 to flask.

6. Place on hotplate and heat at high temperature (approximately 220°C) until about 45 minutes after clearing is completed.

   NOTE: If sample does not clear within 30 minutes to 1 hour, set off, cool, and add more peroxide.

7. Add distilled water to facilitate cooling.

8. Transfer to 250 ml. volumetric flask and take to volume with distilled water.

9. Shake thoroughly, allow to equilibrate, and take aliquot for Auto Analyzer.

Table A-1. Mean percent protein of 24 triticale varieties grown in nine locations.

Variety	Location								
	Huntsville, AL	Tallassee, AL	Experiment, GA	Tifton, GA	Clemson, SC	Marianna, AK	Rohwer, AK	Keiser, AK	Knoxville, TN
AM 4105	10.9	16.1	9.8	11.5	13.0	9.0	8.6	11.3	11.9
ARK 2005	-	15.8	12.8	13.6	12.9	10.1	8.1	9.6	13.8
ARK 2014	10.6	17.9	11.8	12.1	12.0	7.3	8.7	13.4	12.7
ARK 2092	-	17.3	9.6	11.1	11.9	8.8	8.9	13.4	11.9
OK 77842	9.6	17.3	10.5	10.7	11.3	-	10.1	12.7	15.0
AM 3948	12.4	18.0	10.8	11.2	11.4	12.6	8.3	11.7	11.6
6TA 131A	9.0	16.8	13.1	13.7	12.6	10.5	11.3	14.5	14.9
OK 77803	6.3	16.0	12.6	11.8	11.7	7.8	9.9	11.8	14.7
AM 4109	10.0	15.9	10.8	11.1	11.9	8.3	8.4	11.3	11.6
AM 3235	11.8	15.5	11.6	13.1	12.2	10.9	11.9	13.1	13.9
6TA 522	10.8	15.1	14.0	11.6	12.6	10.4	10.8	11.6	12.2
AM 4142	11.1	16.6	10.6	9.2	12.3	10.5	11.1	11.9	12.8
OK 77802	10.1	16.3	11.2	13.1	10.3	8.9	10.3	10.6	12.3
AM 2873	8.6	15.0	13.8	10.9	10.9	9.4	8.2	10.6	11.0
AM 4115	10.2	17.6	10.5	11.3	10.5	11.5	8.5	12.1	11.3
AM 4108	9.6	15.2	12.0	10.6	12.2	8.2	8.2	12.1	11.6
6TA 313	12.0	16.9	9.4	13.1	10.9	9.3	9.1	9.8	11.6
OK 77824	9.5	16.5	11.2	11.0	11.2	9.2	10.1	11.4	12.4
6TA 876	11.6	17.3	12.3	8.8	10.5	10.2	9.3	11.1	12.6
OK 78828	9.1	17.5	-	-	-	9.6	6.5	10.4	-
OK 77801	10.6	15.4	-	-	-	8.4	8.3	12.2	-
OK 77843	11.7	15.6	-	-	-	8.7	8.5	10.6	-
OK 77826	9.0	16.3	-	-	-	9.3	8.6	10.9	-
ARK 2301	9.3	16.6	-	-	-	9.0	7.8	10.5	-

Table A-2. Mean milligrams protein per hundred seed of 24 triticale varieties grown in nine locations.

Variety	Location								
	Huntsville, AL	Tallassee, AL	Experiment, GA	Tifton, GA	Clemson, SC	Marianna, AK	Rohwer, AK	Keiser, AK	Knoxville, TN
AM 4105	342.72	365.70	403.12	453.10	485.61	279.0	334.54	403.41	471.24
ARK 2005	-	383.71	474.58	367.20	537.14	363.6	273.78	381.12	549.24
ARK 2014	354.10	406.35	396.66	428.34	532.04	272.29	334.95	548.06	454.66
ARK 2092	-	338.73	358.64	422.91	608.57	359.04	361.34	562.80	454.58
OK 77842	335.22	404.08	444.70	340.26	473.53	-	453.49	481.33	609.00
AM 3948	430.24	412.24	478.54	516.32	500.40	564.48	390.93	607.23	469.80
6TA 131A	351.01	512.48	521.38	548.00	716.73	480.90	447.48	624.95	639.21
OK 77803	214.60	369.05	468.82	549.88	516.32	297.18	429.66	437.78	618.87
AM 4109	329.96	387.14	351.72	358.53	537.28	344.45	326.76	378.55	392.08
AM 3235	298.36	355.76	376.07	424.44	401.84	364.06	441.49	465.05	444.80
6TA 522	324.36	345.55	504.11	378.16	506.57	338.00	408.24	342.20	442.86
AM 4142	398.42	425.23	412.70	391.92	593.40	324.45	422.91	481.95	441.60
OK 77802	381.54	379.96	452.68	517.45	459.96	299.93	471.74	351.92	544.89
AM 2873	302.75	356.76	585.42	565.71	526.91	397.62	359.16	468.52	453.20
AM 4115	404.20	396.38	442.21	453.13	542.56	484.15	374.00	502.15	518.67
AM 4108	367.86	409.31	478.53	435.66	665.44	300.12	410.00	498.52	548.68
6TA 313	360.70	377.24	381.25	500.42	455.47	325.50	345.80	313.60	467.48
OK 77824	335.92	379.70	444.08	405.90	475.17	352.36	369.66	403.56	522.04
6TA 876	289.56	362.40	456.07	312.40	397.81	308.04	300.39	286.38	405.72
OK 78828	290.58	327.48	-	-	-	362.88	352.95	558.48	-
OK 77801	310.10	328.18	-	-	-	273.00	357.73	469.70	-
OK 77843	374.04	326.31	-	-	-	239.25	344.25	454.74	-
OK 77826	251.56	327.51	-	-	-	268.77	388.72	391.31	-
ARK 2301	271.18	376.45	-	-	-	351.90	273.00	452.55	-

Table A-3. Mean weight per hundred seed (grams) of 24 triticale varieties grown in nine locations.

Variety	Location								
	Huntsville, AL	Tallassee, AL	Experiment, GA	Tifton, GA	Clemson, SC	Marianna, AK	Rohwer, AK	Keiser, AK	Knoxville, TN
AM 4105	3.14	2.27	4.10	3.94	3.74	3.10	3.89	3.57	3.96
ARK 2005	-	2.41	3.70	2.70	4.15	3.60	3.38	3.97	3.98
ARK 2014	3.36	2.26	3.35	3.54	4.54	3.73	3.85	4.09	3.58
ARK 2092	-	1.96	3.74	3.81	5.15	4.08	4.06	4.20	3.82
OK 77842	3.54	2.33	4.24	3.18	4.20	-	4.49	3.79	4.06
AM 3948	3.48	2.31	4.40	4.61	4.43	4.48	4.71	5.19	4.05
6TA 131A	3.90	3.05	3.98	4.00	5.70	4.58	3.96	4.31	4.29
OK 77803	3.40	2.30	3.72	4.66	4.44	3.81	4.34	3.71	4.21
AM 4109	3.32	2.43	3.26	3.23	4.53	4.15	3.89	3.35	3.38
AM 3235	2.56	2.29	3.23	3.24	3.33	3.34	3.71	3.55	3.20
6TA 522	2.99	2.24	3.62	3.26	4.00	3.25	3.78	2.95	3.63
AM 4142	3.56	2.57	3.90	4.26	4.82	3.09	3.81	4.05	3.45
OK 77802	3.78	2.35	4.05	3.95	4.53	3.37	4.58	3.32	4.43
AM 2873	3.52	2.38	4.26	5.19	4.81	4.23	4.38	4.42	4.12
AM 4115	3.90	2.25	4.20	4.01	5.20	4.21	4.40	4.15	4.59
AM 4108	3.84	2.69	4.00	4.11	5.50	3.66	5.00	4.12	4.73
6TA 313	3.02	2.23	4.04	3.82	4.19	3.50	3.80	3.20	4.03
OK 77824	3.52	2.31	3.96	3.69	4.21	3.83	3.66	3.54	4.21
6TA 876	2.54	2.12	3.69	3.55	3.80	3.02	3.23	2.58	3.22
OK 78828	3.18	1.90	-	-	-	3.78	5.43	5.37	-
OK 77801	2.93	2.13	-	-	-	3.25	4.31	3.85	-
OK 77843	3.20	2.09	-	-	-	2.75	4.05	4.29	-
OK 77826	2.84	2.01	-	-	-	2.89	4.52	3.59	-
ARK 2301	2.94	2.27	-	-	-	3.91	3.50	4.31	-

VITA

Weyman Parkman Fussell, Jr. was born in Atlanta, Georgia on 28 July 1945. He graduated from Gordon High School in that city in 1963. He entered The University of Tennessee, Knoxville in September 1963, and in June 1968 received a Bachelor of Science degree in Electrical Engineering.

In September 1974 after working in Brazil for two and one-half years as a Peace Corps volunteer, he returned to the United States and accepted a research assistantship at Purdue University for study toward a Master's degree in Plant Breeding. This degree was awarded in August 1976.

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