GAS LOSS: ITS MEASUREMENT, HERITABILITY, AND ASSOCIATION WITH OTHER QUALITY TRAITS IN TWO POPULATIONS OF COMMON WHEAT

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CHAPTER I

INTRODUCTION

Since the majority of hard red winter wheat produced in the United States of America is consumed as bread, the baking quality of wheat flour is a factor of vital importance to breeders and cereal chemists concerned with the development of improved varieties. Quality tests on the physical and chemical properties of wheat and wheat flour play an important role during the breeding, selection and evaluation of experimental lines. However, the chemical tests, which give information about the composition of wheat flour, are somewhat limited, because the relation between chemical composition and baking quality is not perfectly understood. The physical tests (sedimentation test, mixograph, etc.) serve to indicate the relative baking value of different flours. Therefore, satisfactory evaluation of experimental lines can be made only after actual baking tests.

The ability of a wheat flour to produce a large and good-textured loaf primarily depends on the production of gas within the dough and the retention of a high proportion of this gas during the baking process. Gas production is the result of the joint effects of the diastatic enzymes of both flour and yeast. Gas retention is a function of the quantity and quality of gluten.

Extensive research has been done on gas retention as well as other quality characteristics. However, almost all of the research on gas

retention has been devoted to measurements of gas retention or gas loss. There has been little or no work relating to gas retention properties of different wheat genotypes which is applicable to breeding programs. In order to evaluate experimental lines for their gas-retaining powers, a suitable laboratory procedure is needed. A method of measurement needs to be developed for testing small samples and this test could then be applied to breeding lines to evaluate the genetic system underlying this trait and to determine the association of gas retention with other important quality factors. It is important for the researcher to know the genetic control of this trait as well as its environmental influences, association with other characters in order to develop varieties with high gas retention properties.

The objectives of this research problem were (1) to develop suitable procedure for measuring gas retention on breeding samples, (2) to determine the effects of genotype and environment on gas retention and other quality traits, and (3) to study the association among important quality traits including gas retention.

Each of these topics is presented in a separate chapter, with some modifications in the style and form required by the scientific journals in the author's field.

CHAPTER II

MATERIALS AND METHODS

Genetic Material and Field Procedures

Two sets of genetic material of hard red winter wheat, Triticum aestivum L. em. Thell, ssp vulgare (Vill., Host) Mackey., were utilized in this study. One set, hereafter referred to as the "progeny set," consisted of 59 lines of hard red winter wheat derived from the cross of Triumph with C.I. 12406. The other set, hereafter referred to as the "variety set," consisted of six hard red winter wheat varieties.

The progeny set. Triumph, one of the parents of the progeny set of lines, has been described as a very early, mellow gluten type variety (24). It was developed by Mr. Joseph Danne, El Reno, Oklahoma, and released in 1940. It is widely grown in the state. Triumph is characterized by a short mixing time and low mixing tolerance (117). The other parent of the progeny set was C.I. 12406. The parentage of C.I. 12406 is Marquillo/Oro//Oro/Tenmarq. It is an experimental strain developed by the Kansas Agricultural Experiment Station and has strong gluten properties and long mixing time. C.I. 12406 was judged acceptable by the milling and baking trade in collaborative testing, but was not released because of certain agronomic deficiencies (117). Representative quality data of these two parents are presented in Table I along with Comanche, Kaw 61, and Scout for comparison. The cross of

TABLE I

AVERAGE QUALITY DATA OF PARENTS, CHECKS, AND PROGENY GROWN AT STILLWATER, 1968 AND 1969

Character	Unit of Measurement	Triumph	C.I. 12406	Comanche	Kaw 61	Scout	Tmp/C.I. 12406 Progeny
Gas loss	cc	7.17	7.46	6.50	9.21	7.92	7.57
Pearling index	%	43.9	51.5	51.4	52.1	51.4	47.7
Test weight	lb/bu	60.2	59.2	57.5	62.4	58.3	59.5
Wheat protein	%	12.7	13.3	13.3	12.0	12.7	12.9
Wheat ash	%	1.45	1.57	1.58	1.42	1.45	1.45
Flour yield	%	65.7	67.6	70.8	68.6	68.1	67.5
Flour protein	%	11.4	11.6	11.7	10.4	11.4	11.4
Flour ash	%	0.37	0.38	0.39	0.39	0.40	0.39
Sedimentation value	cc[1]	52.3	55.9	51.3	38.0	49.8	53.6
Specific sedimentation	cc/%	4.49	4.32	4.78	3.51	4.25	4.60
Mixing time	min.	2:57	6:27	3:35	4:44	3:01	4:11
Mixing curve height	cm	14.1	13.5	14.7	12.8	15.7	14.5

[1]In 1969, 2.3 g flour samples were tested instead of the usual 3.2 g samples. Therefore, the average of two years is low.

Tmp/C.I. 12406 was made in the Spring of 1954. A total of 112 plants were produced in the F_2 and these were then grown as unselected F_2 subpopulations in the F_3 and F_4 generations in a study conducted by Schlehuber et al. (117). For the present study, 59 F_2 subpopulations of this cross were grown in 1968 and 1969 as F_5 and F_6 generations respectively. Also included in the tests were the two parents and three check varieties: Comanche, Kaw 61, and Scout.

The design of the experiment was an 8 x 8 triple lattice. Plots consisted of 4 rows, 3 m long and 30 cm apart. The seeding rate was 70 kg/ha. The two center rows of 2.4 m of each plot were harvested for yield, and for the determinations of test weight, thousand kernel weight, and pearling index. The two outside rows of each plot were also harvested and grain from these rows was later combined with that from the two center rows to obtain sufficient amounts of grain for the other quality tests.

In 1968, the threshed, cleaned grain samples were fumigated with a mixture of ethylene dichloride, methyl bromide, and carbon tetrachloride (29.0, 7.2, and 63.8% respectively). The fumigated samples were aired to remove the fumigant and 300 g samples were stored in polyethylene bags at 1.1 C until quality analyses were conducted nearly a year after harvest. The quality analyses of the 1969 material were completed within two months after the harvest. For that reason the 1969 samples were not fumigated, but were stored at 1.1 C immediately after the threshing operation.

The variety set. Six hard red winter wheat varieties were selected for this phase of the study where larger samples of grain were required. These varieties were Triumph, Kaw 61, Scout, Sturdy, Tascosa, and

Warrior. Detailed descriptions of these varieties can be found in the following references (4, 69, 82, 83, 99). Representative quality data of these varieties, based on samples grown at three locations in 1968 and 1969, are given in Table II.

These varieties were grown in randomized complete block designs in 1968 and 1969 at 3 locations Cherokee, Goodwell (irrigated test), and Muskogee with the 3 replications of each location. The size of an individual plot was approximately 3 m x 20 m. The plots were seeded at an approximate rate of 70 kg/ha.

The seed harvested from each plot was cleaned, and a 2000 g sample was taken for the milling and baking tests. The 1968 samples were fumigated as described for the progeny set and stored at 1.1 C until the quality analyses were conducted. The 1969 samples were stored at 1.1 C without fumigation.

Laboratory Methods

Gas loss for each sample was determined by a procedure developed in connection with this study. A detailed description of the apparatus and method is given in Chapter III. Tests were run on duplicate 10 g samples of fermented dough and gas loss was expressed as the average gas loss value per sample.

Pearling index tests were run on triplicate 10 g grain samples by a Strong-Scott barley pearler following the procedure described by Yildirim (136). Test weight was measured by the standard procedure accepted by the United States Department of Agriculture (128). These two tests were completed immediately after the samples were harvested and threshed.

TABLE II

AVERAGE QUALITY DATA OF SIX VARIETIES GROWN AT CHEROKEE, GOODWELL, AND MUSKOGEE, 1968 AND 1969

Character	Unit of Measurement	Triumph	Kaw 61	Scout	Sturdy	Tascosa	Warrior
Gas loss	cc	7.58	9.64	8.68	7.69	8.44	7.36
Pearling index	%	41.6	49.6	50.7	48.2	48.4	53.4
Test weight	lb/bu	59.9	61.1	58.6	58.2	60.3	57.1
Wheat protein	%	12.9	12.3	12.9	13.6	13.1	12.4
Wheat ash	%	1.63	1.62	1.59	1.70	1.60	1.57
Flour yield	%	67.0	67.9	67.4	66.8	68.0	68.0
Flour protein	%	11.5	10.9	11.4	12.2	11.5	10.9
Flour ash	%	0.41	0.41	0.41	0.43	0.41	0.42
Sedimentation value	cc	48.8	41.4	45.8	45.9	53.7	44.7
Specific sedimentation	cc/%	4.18	3.78	4.00	3.72	4.60	4.04
Mixing time	min.	2:28	4:13	2:51	3:20	4:05	3:09
Mixing curve height	cm	17.2	15.7	16.8	17.2	16.3	15.5
Loaf volume[1]	cc	772	741	769	827	799	803

[1]Without bromate

The analyses for the other quality traits were run on the 1968 grain samples in April and May 1969 and on the 1969 grain samples in September and October, 1969. The wheat samples were removed from cold storage about 2 days prior to milling to allow them to come to mill-room temperature. Milling of the progeny set samples was performed on a Brabender quadramatic senior mill. The variety set samples of 1968 were milled on a Bühler pneumatic mill and milling of the 1969 variety samples was performed on a Brabender quadramatic senior mill. The flours obtained from both mills were straight grade flours. For the variety set samples, each flour sample was thoroughly blended and a subsample was removed for analyses. The bulk of the flour was then stored at 1.1 C until the baking tests.

The following analyses and tests were made on these variety set subsamples as well as on the progeny set samples: (a) moisture, (b) ash, (c) protein, (d) mixograph, (e) sedimentation, and (f) gas retention. Analyses of ground wheat and flour samples were performed by standard methods, according to AACC cereal laboratory methods (2). All analyses and tests were performed at the Milling and Baking Laboratory of the Oklahoma Agricultural Experiment Station, Stillwater, Oklahoma. The boric acid modification of the Kjeldahl procedure was employed for the protein analyses on 1 g samples. Wheat ash was determined on 3 g samples, flour ash on 5 g samples. Sedimentation tests were run according to the procedure described by Pinckney et al. (113) on 3.2 g flour samples for the 1968 samples. For the 1969 samples, 2.3 g flour samples were used for the sedimentation test. Mixogram tests were run on 35 g flour samples. Baking tests were conducted applying the standard procedure with the exception that bromate was omitted.

Statistical Analyses

The data of the triple lattice for the progeny set grown at Stillwater were analyzed by the procedures given by Cochran and Cox (31), Cox et al. (35), Hayes and Immer (66), and Homeyer et al. (70). The efficiency of the triple lattice for gas loss was found to be 100 and 106% in 1968 and 1969 respectively. Although the efficiency of the triple lattice design for the other quality traits (protein content, sedimentation value, specific sedimentation, and mixing curve height) was high, the data of this experiment was analyzed as randomized complete block design with three blocks, since the main purpose for employing the triple lattice was to minimize the variation which might be due to the day-effect during the determination of gas loss.

Standard analyses of variance were conducted on both the progeny and variety set. Estimates of phenotypic and genotypic variances and correlation coefficients were performed by variance component method, according to the procedures given by Johnson et al. (80, 81), Miller et al. (111), and Wallace et al. (129).

Estimates of Phenotypic and Genotypic Variances

Estimates of the phenotypic and genotypic variances for the quality traits studied were obtained from the following analyses of the progeny and variety sets.

(a) From the separate analyses of F_5 and F_6 generations of the progeny set.

(b) From the combined analysis of F_5 and F_6 generations of the progeny set.

(c) From the separate analyses of each location and year of the variety set.

(d) From the combined analyses of locations in one year of the variety set.

(e) From the combined analyses of years at one location of the variety set.

(f) From the combined analysis of locations and years for the variety set.

Analyses of the data were based on the assumption that performance as measured in any of the traits considered was composed as indicated in the following equation:

$$X_{ijkm} = u+g_i+l_j+y_k+b_{jkm}+(ly)jk+(gl)_{ij}+(gy)_{ik}+(gly)_{ijk}+e_{ijkm}$$

where X_{ijkm} = the measured value from the i^{th} genotype, j^{th} location, k^{th} year and m^{th} plot

u = overall mean

g_i = effect due to the i^{th} genotype

l_j = effect due to the j^{th} location

y_k = effect due to the k^{th} year

b_{jkm} = effect due to the m^{th} block at the j^{th} location in the k^{th} year

$(ly)_{jk}$ = effect due to the interaction of j^{th} location and k^{th} year

$(gl)_{ij}$ = effect due to interaction between genotypes of the i^{th} line and environments of the j^{th} location

$(gy)_{ik}$ = effect due to the interaction between genotypes of the i^{th} line and environments of the k^{th} year

$(gly)_{ujk}$ = effect due to the interaction between the genotypes of the i^{th} line and environments of the j^{th} location with the environments of the k^{th} year.

e_{ijkm} = a composite of remaining effects (including plot error, sampling error, and error of measurement).

The general model given above is reduced as follows when:

(a) $y < 2$ $\quad X_{ijm} = u + g_i + l_j + b_{jm} + (gl)_{ij} + e_{ijm}$

(b) $1 < 2$ $\quad X_{ikm} = u + g_i + y_k + b_{km} + (gy)_{ik} + e_{ikm}$

(c) $y,1 < 2$ $\quad X_{im} = u + g_i + b_m + e_{im}$

It is important to emphasize that the genotypic effect g, reflects the genotypic value of a line as an average for the population of environments (locations and years) in which the data obtained were considered to be a sample. Mean squares given in Table III were equated to their corresponding expectations and the estimates of variance components were solved from the suitable equations. Population variances were symbolized by σ^2 and their subscripts indicate the source. In this study, σ^2 was used as the estimate of a parameter. The estimates of variance components were substituted for their parameters in the following formula to obtain the estimate of phenotypic variance:

$$\sigma^2 ph = \sigma^2 g + \sigma^2 gl/l + \sigma^2 gy/y + \sigma^2 gly/ly + \sigma^2 e/rly$$

The estimates of heritability in the broad sense were obtained from the following general formula:

$$H = \sigma^2 g/\sigma^2 ph$$

TABLE III

FORM OF VARIANCE ANALYSIS AND MEAN SQUARE EXPECTATIONS

Source	df	MS	Mean Square Expectations
A. Analysis for data from one location in one year:			
Varieties (or lines)	n-1	I	$\sigma^2e + r(\sigma^2gyl + \sigma^2gl + \sigma^2gy + \sigma^2g)$
Error	(r-1)(n-1)	II	σ^2e
B. Analysis for data from two or more years in one location:			
Varieties (or lines)	n-1	I	$\sigma^2e + r(\sigma^2gly + \sigma^2gy) + ry(\sigma^2gl + \sigma^2g)$
Varieties x years	(n-1)(y-1)	II	$\sigma^2e + r(\sigma^2gly + \sigma^2gy)$
Error	y(n-1)(r-1)	III	σ^2e
C. Analysis for data from two or more locations in one year:			
Varieties	n-1	I	$\sigma^2e + r(\sigma^2gly + \sigma^2gl) + rs(\sigma^2gy + \sigma^2g)$
Varieties x locations	(n-1)(s-1)	II	$\sigma^2e + r(\sigma^2gly + \sigma^2gl)$
Error	s(n-1)(r-1)	III	σ^2e
D. Analysis for data from two or more years in two or more locations:			
Varieties	n-1	I	$\sigma^2e + r\sigma^2gly + rs\sigma^2gl + ry\sigma^2gy + rsy\sigma^2g$
Varieties x years	(n-1)(y-1)	II	$\sigma^2e + r\sigma^2gly + ry\sigma^2gy$
Varieties x locations	(n-1)(s-1)	III	$\sigma^2e + r\sigma^2gly + rs\sigma^2gl$
Varieties x locations x years	(n-1)(y-1)(s-1)	IV	$\sigma^2e + r\sigma^2gly$
Error	ys(n-1)(r-1)	V	σ^2e

However, since the mean square expectations for estimates of genotypic variance differ according to type of analysis used, the heritability estimates are different for each set of experiments as follows:

(a) for the single experiments (one year and one location):

$$H = \frac{(\sigma^2 g + \sigma^2 gl + \sigma^2 gy + \sigma^2 gly)}{\sigma^2 g + \sigma^2 gl + \sigma^2 gy + \sigma^2 gly) + \sigma^2 e/r}$$

(b) for one location in two or more years:

$$H = \frac{(\sigma^2 g + \sigma^2 gl)}{(\sigma^2 g + \sigma^2 gl) + (\sigma^2 gy + \sigma^2 gly)/y + \sigma^2 e/ry}$$

(c) for two or more locations in one year:

$$H = \frac{(\sigma^2 g + \sigma^2 gy)}{(\sigma^2 g + \sigma^2 gy) + \sigma^2 gl + \sigma^2 gly)/l + \sigma^2 e/rl}$$

(d) for two or more locations and years:

$$H = \frac{\sigma^2 g}{\sigma^2 g + \sigma^2 gy/y + \sigma^2 gl/l + \sigma^2 gly/ly + \sigma^2 e/rly}$$

Estimates of Phenotypic and Genotypic Correlations

Estimates of the phenotypic and genotypic correlations between quality traits were obtained from the following analyses of progeny and varieties:

(a) From the separate analyses of F_5 and F_6 generations of the progeny set.

(b) From the combined analysis of F_5 and F_6 generations of the progeny set.

(c) From the combined analysis of locations and years for the variety set.

Phenotypic and genotypic correlations for the two populations studied were based on line or variety means. Covariance analyses between the quality traits followed the same form as the variance analyses shown in Table III. The procedure given by Kempthorne (91) was applied to obtain mean products between two traits by assuming that the variance of a variable constructed from two variables by addition contains the variances of two variables plus twice the covariance.

New variables were formed by adding the quality traits in pairs. The analysis of variance was performed and the covariance of corresponding source was found. The mean square expectations of the covariance analysis are analogous to the mean square expectations for the analysis of variance. The mean product of lines or varieties for the traits Y and X obtained from the analysis of covariance was considered to be an estimate of the phenotypic covariance of two traits. The phenotypic correlation between the quality traits was then obtained by the following formula:

$$r_{ph} = \frac{MPL(Y,X)}{MSL(Y)\ MSL(X)}$$

where MPL(Y,X) = line (or variety) mean product for the traits Y and X,

MSL(Y) and MSL(X) = line (or variety) mean square for the trait Y and for the trait X respectively.

Genotypic correlation for the traits Y and X was calculated in a similar manner by using formula given by Johnson et al. (81) and Miller et al. (111) as follows:

$$rg = \frac{COVg(Y,X)}{\sigma^2 g(Y)\ \sigma^2 g(X)}$$

where COVg(Y,X) = genotypic covariance between Y and X, $\sigma^2 g(Y)$, and $\sigma^2 g(X)$ = genotypic variances of Y and X respectively.

CHAPTER III

GAS LOSS: ITS DETERMINATION AND EVALUATION AS A QUALITY TRAIT

Gas loss has been accepted as an indirect index of gas retention (9, 10, 21). Many researchers have mentioned the importance of gas retention as it relates to bread quality (5, 17, 21, 23, 34, 57, 72, 124, 132) and it has been generally accepted that flour strength is correlated with gas retention (5, 72, 75, 130, 131). Bailey (5) defined the strength of flour as the ratio between the rate of gas production in, and the rate of loss of CO_2 from, the fermenting mass of dough. Clark (30) summarized the definitions of fermentation tolerance as the proper balance between gas production and retention. Gas retention has been related to the colloidal structure of the dough (39, 126).

It was speculated that the gas nucleus, from which the bubble originates, starts in a glutinous core. As the bubble expands, the gluten from the starch-gluten matrix of the endosperm is drawn out (11, 12). The properties of the gas bubbles are determined by those properties of gluten which cause it to retain its integrity. Radii of gas bubbles vary from 10^{-4} cm to 10^{-3} cm and the expansion of gas cells was estimated by means of diffusion of dissolved gas through the batter between two cells (20, 61).

Apparently, gas retention depends on the balance of several properties of a dough (21). Oxidizing flour improvers may increase gas

retention (6, 45, 57, 79, 103). The consistency of dough and mixing time also affects gas retention (95, 103). The effects of alcohol and water treatments, phosphates, and aluminum on gas retention are also reported (21, 77).

Several methods have been employed to determine the degree of gas retention during fermentation and proofing periods. In principle most of the methods for the determination of gas production can be modified to measure gas retention in the dough by absorbing the escaping CO_2 in an alkali (21). A majority of the measurement methods require simultaneous measurements of gas production and volume increase from equal amounts of doughs treated under similar conditions. Since workers have used several different methods to measure gas retention, gas retention values have been expressed in different terms and units. Bailey and Weighley (10) adopted an indirect approach and determined the amount of gas that escaped from the dough by absorbing it in a known amount of a barium hydroxide solution. Johnson (77) and Bailey and Johnson (9) passed the carbon dioxide escaping from the dough through an indicator solution and determined the rate at which CO_2 escaped.

Reviews of the methods to measure gas retention have been given by Bloksma and Hlynka (21), Dunlop (40), Johnson (77), and Kent-Jones (92). The volumetric measurement of gas loss is based on the assumption that equal amounts of liquid are displaced by the volume increase of carbon dioxide. The escaping gas is measured by the volume of the liquid displaced from a gas burette or from a closed system connected to an airtight vessel containing a piece of dough. This is defined as gas production. Gas retention is expressed as the volume of the displaced liquid from a second gas burette which is connected to another

airtight dough container having the same amount of dough plus a strong KOH solution. The difference between the gas production and gas retention is defined as the gas loss (5, 77, 95).

A simple volumetric method was employed by Jago (74) to measure gas production and retention. This type of measurement method has been improved and used by many workers (43, 47, 67, 71, 72, 73, 75, 86, 95, 106, 122, 130, 131). Bailey and Johnson (9) described a volumetric method which has been used widely. They measured the expansion of dough plus the escaped CO_2 by the volume of the liquid displaced from a burette connected to a Mason jar containing dough and 23% NaCl solution. The expansion of dough was recorded by the volume change from a second burette connected to a second Mason jar which contained dough and a 23% KOH solution. The difference between the two readings was defined as the volume of CO_2 which had escaped from the dough during the interval of measurement. This type apparatus has been employed and modified by several researchers (2, 6, 7, 15, 40, 42, 54, 78, 79, 86, 95, 97, 104, 120, 121).

Irvin (73) described an improvement based on "Mariotte's bottle" in which the gas in the dough vessel remains at constant pressure. Hullett (71) prevented the gas from going into solution in the water by enclosing the inlet tube in another containing a liquid in which the CO_2 is insoluble. This permitted the avoidance of salt solutions.

Another method is based on the pressure increase in an airtight container of known volume. The pressure is measured by means of a mercury column or by pressure gauges. This manometric method and its modifications have been employed by some workers (18, 19, 36, 38, 93, 101, 107, 114, 115, 116).

The Chopin zymotachygraphe which records the pressure in cycles of 2.5 minutes with and without escaped CO_2 has been used to measure gas production and gas retention (26, 27, 28, 29). The Chefaro balance was described as an instrument to record gas production and gas retention automatically during the course of fermentation (44, 45, 46, 47).

The fermentograph, which was described by Brabender (22), has also been used in studies of gas retention. Another instrument for recording gas production and gas retention is the volumetrograph which works on the principle of a gasometer (92). Marek and Bushuk (102), Marek et al. (103) and Seibel and Crommentuyn (119) reported a modified Brabender oven rise recorder to measure the degree of gas retention. Glabe (59) described another fermentometer system utilizing the manometric and volumetric features of previous methods.

Additional methods to measure gas production and retention have been reported (60, 76, 85, 96, 108, 110, 112, 127, 133). A micro test, which measures the expansion of dough, was employed by Elling and Barmore (48) to measure gas retention at 45 C. This type of measurement has been reported by others (84, 109, 110). Kent-Jones (92) described the Fornetograph which has been used in Germany, and a Swedish instrument known as the S.I.A. Comparative studies of manometric, fermentograph and volumetric methods have been made (41, 49, 118). All three methods gave satisfactory results.

As a useful quality trait, gas retention should be related to dough strength. Simple correlations between gas retention and loaf volume have been reported (40, 48, 56, 77). Geddes (56) reported a correlation between loaf volume and gas retention with r values ranging from 0.866 to 0.947. He found that the highest r value was between

loaf volume with bromate added and the gas retention capacity of the dough observed. Dunlop (40) reported a significant correlation between gas retention and loaf volume with an r value of 0.94 in kneaded doughs. He did not find correlation between gas retention and loaf volume in unkneaded doughs. Miller et al. (110) reported r values from 0.81 to 0.90 between gas retention measured by dough expansion and loaf volume. Jongh (84) found a significant correlation with an r value of 0.84 for these two traits. Harris and Sibbitt (63) reported r values of -0.365 and 0.601 for North Dakota and Mexican wheat selections respectively between gas retention measured by dough expansion and loaf volume. Elling and Barmore (48) reported significant correlation between gas retention and loaf volume with r values ranging from 0.71 to 0.95. A close association of gas retention and loaf volume has been reported by some early workers without giving any correlation coefficient (72, 106, 129, 130).

Elling and Barmore (48) reported a significant correlation between gas retention and protein content with r values ranging from 0.87 to 0.92. Harris and Sibbitt (63) found insignificant correlation between these two quality traits. They also reported an r value of 0.67 for the correlation between gas retention and sedimentation value. Gfeller and Whiteside (58) reported r values from 0.49 to 0.69 for the correlation between dough expansion and sedimentation value. They found r values ranging from 0.46 to 0.74 for the correlation between dough expansion and mixing time.

Results and Discussion

Although most of the previous work reported on gas retention has been conducted at temperatures of less than 35 C, gas loss measured at higher temperatures after normal fermentation will be closer to the conditions encountered during the actual baking process. The objectives of this phase of the present study were to measure gas loss at elevated temperatures and to evaluate it as a quality trait.

Apparatus

After considerable experimentation, the apparatus employed for the determination of gas retention (as measured by gas loss) was based on the volumetric method reported by Bailey and Johnson (9). Two modifications proposed by Irvin (73) and Hullett (71) were applied in this study to the basic apparatus described by Bailey and Johnson (9), Dunlop (40), and Johnson (77). One of these modifications consisted of a Mariotte's bottle used to prevent pressure changes in the dough vessel. The other modification consisted of enclosing the inlet tube in a large tube containing a heavy liquid (Diethyl phthalate) to prevent the escaping CO_2 from going into solution. After these modifications, the apparatus consisted of two parts: (a) dough container, and (b) displacement chamber.

(a) Dough container. Half-pint Mason jars were employed as dough containers. Size 12 rubber stoppers were used to seal the jars instead of self-sealing brass lids. A glass tube of 0.3125 cm in diameter was inserted through each stopper as an outlet tube in order to carry the produced gas to the displacement chambers. The Mason jars

were belted with a lead band of approximately 230 g to keep them stationary in the water bath.

(b) Displacement chamber. Two types of displacement chambers were employed: one for the measurement of gas production (type 1) and the other for the measurement of dough expansion (type 2). One pint Mason jars were employed for both types. The displacement chamber of type 1 used in these studies is shown in Figure 1. It was based on the modification given by Hullett (71). The arrangement of the second type displacement chamber was based on the modification given by Irvin (73) and it is shown in Figure 2.

A unit of the apparatus which measured the gas loss consisted of two dough containers and two displacement chambers of types 1 and 2. The dough container holding a dough sample and a 23% NaCl solution was connected to a type 1 displacement chamber. The other dough container holding a dough sample and a 23% KOH solution was connected to a type 2 displacement chamber (Fig. 3).

The difference between the volumes of the displaced water from type 1 and type 2 displacement chambers is the measure of gas loss. This is an indirect index of gas retention. A low gas loss value indicates a high degree of gas retention.

Measurement of Gas Loss

The majority of gas retention measurements reported in the literature were performed during fermentation periods in a temperature range of 28 to 35 C. Also, according to reports of previous investigators, dough containers were generally connected to displacement chambers after a 10 to 15 minute waiting period under the assumption that air

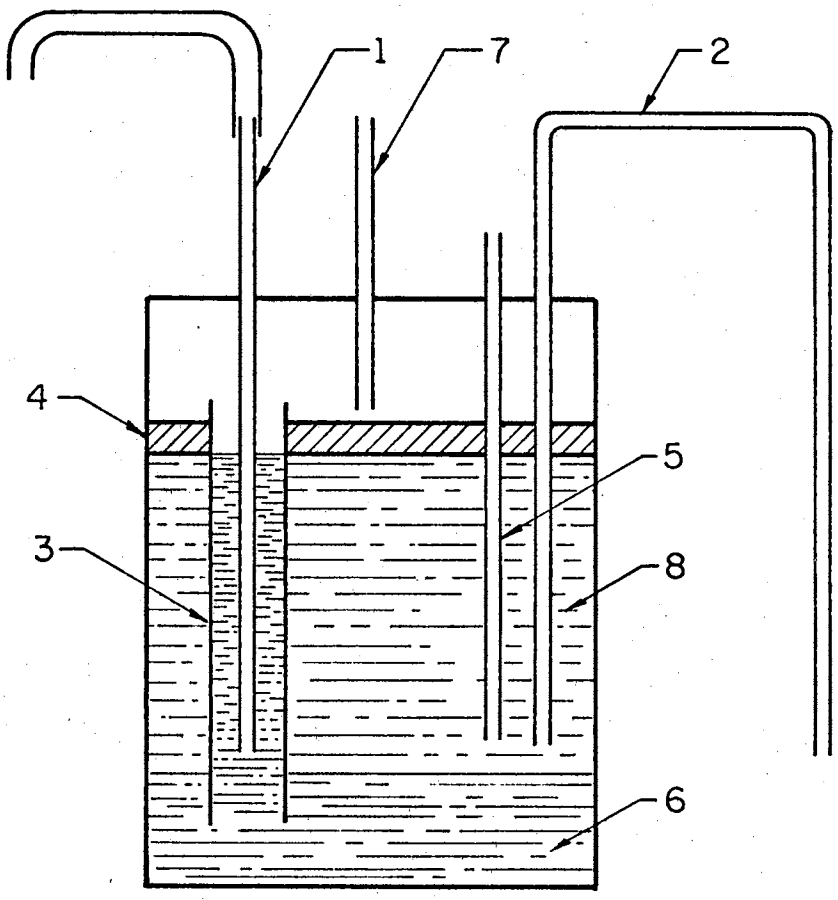

Figure 1. Type 1 Displacement Chamber. (1) Inlet Tube, (2) Outlet Tube, (3) Glass Tube for Heavy Liquid, (4) High Vacuum Oil Layer, (5) Refilling Tube, (6) Diethyl Phthalate Layer, (7) Gas Escape Outlet, (8) Distilled Water.

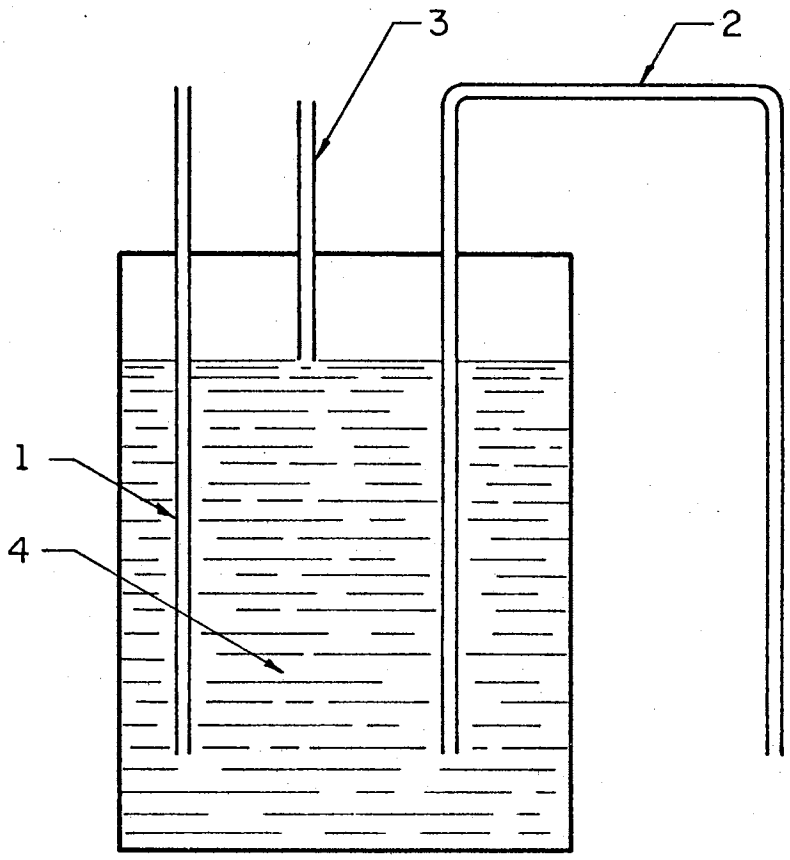

Figure 2. Type 2 Displacement Chamber. (1) Inlet Tube, (2) Outlet Tube, (3) Gas Escape Outlet, (4) Distilled Water.

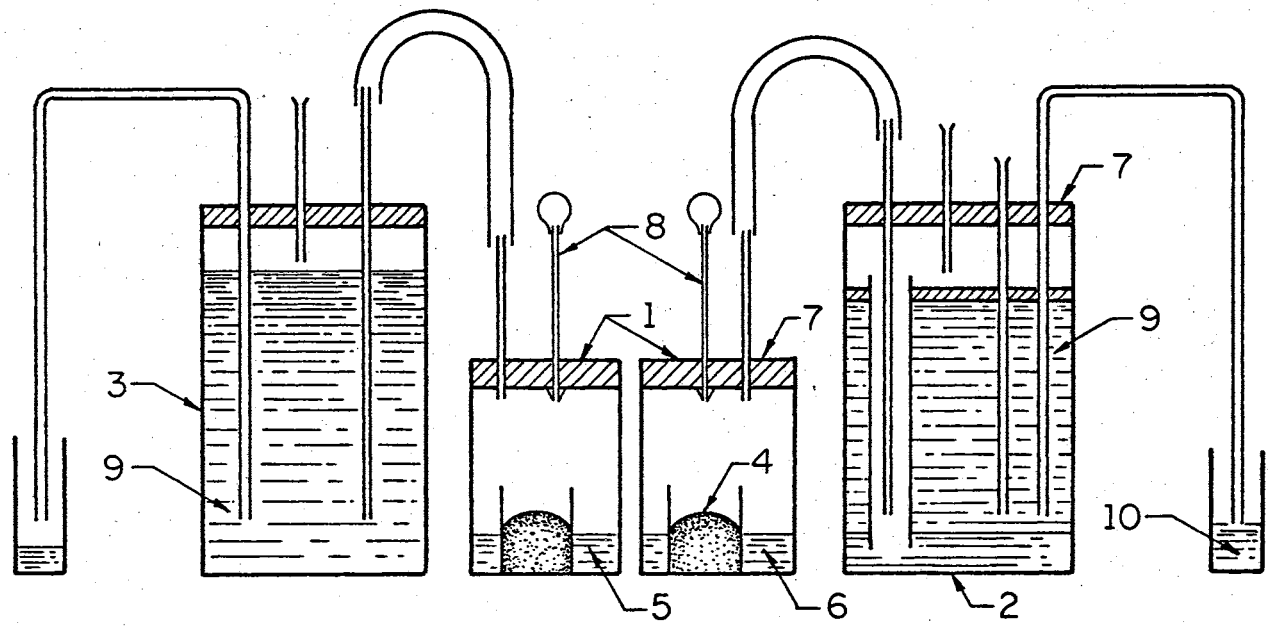

Figure 3. A Unit of the Apparatus to Measure Gas Loss. (1) Dough Containers, (2) Type 1 Displacement Chamber, (3) Type 2 Displacement Chamber, (4) Dough, (5) KOH Solution, (6) NaCl Solution, (7) Rubber Stopper, (8) Stopper Hooks, (9) Distilled Water, (10) Displaced Water.

expansion in the containers were reduced to 0 with this procedure. In the present study it was decided to measure gas loss at elevated (50 to 55 C) temperature and to determine the effects of air expansion and fermentation time on gas production and retention.

The Effect of Air Expansion on Gas Loss Measurements

Since the water displacement measurements may be affected by the expansion of air in the dough containers, experiments were conducted in the absence of dough samples to study this possibility. Dough containers respectively containing 25 ml NaCl and KOH solutions were connected to displacement chambers at 5, 10, and 15 minute intervals. The water displacement during a 1-hour period was recorded at 15 minute intervals. The results of this experiment are shown in Table IV. From this table, it can be seen that the water displacement due to air expansion was relatively high when the connections were made after the five minute waiting period. The water displacement for the 5-minute waiting period was almost twice as great as the displacement for the 10-minute waiting period and nearly three times as great as the displacement for the 15 minute period. From Table IV it is also observed that water displacement between two dough containers having NaCl and KOH solutions were not different.

Consequently, during the subsequent measurements of gas loss, the 15-minute waiting period was used. Under the 15-minute waiting period the measurements of gas production and dough expansion would be increased by 6.5 cc due to air expansion. If dough expansion is accepted as an index of gas retention, then the pressure increase due to air

TABLE IV

WATER DISPLACEMENT IN CC FROM THE DISPLACEMENT CHAMBERS DUE TO AIR EXPANSION AT 55 C

Recording Time (Min.)	Waiting Period Before Connection								
	5 Min.			10 Min.			15 Min.		
	NaCl	KOH	Avg.	NaCl	KOH	Avg.	NaCl	KOH	Avg.
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	13.0	12.0	12.5	7.0	7.0	7.0	5.0	5.0	5.0
30	17.0	15.0	16.0	9.0	10.0	9.5	6.0	5.0	5.5
45	17.0	15.0	16.0	9.5	10.0	9.7	7.0	6.0	6.5
60	17.0	15.0	16.0	10.0	11.0	10.5	7.0	6.0	6.5

expansion is also included. When gas loss is employed as an index of gas retention the effect of air expansion on this index is eliminated if it is assumed that the containers having NaCl and KOH solutions displace the same amount of water due to air expansion as it was observed in Table IV. The measured gas production can best be expressed by the following equation:

$$\text{Gas production (cc)} = \text{Air expansion} + \text{actual dough expansion} + CO_2 \text{ escaped from the dough} \quad (1)$$

The observed dough expansion can be expressed by the following equation:

$$\text{Apparent dough expansion} = \text{Air expansion} + \text{actual dough expansion} \quad (2)$$

Because the CO_2 escaping from the dough is absorbed by the KOH solution, it is not included in equation 2. Therefore, gas loss is the difference between equation 1 and equation 2 and is free of the bias due to air expansion.

The Effect of Fermentation Time on Gas Production and Gas Retention

Laboratory tests were conducted to determine the effects of fermentation time on gas production and gas loss. Observed gas production, dough expansion and calculated gas loss for various fermentation periods are given in Table V. These tests were conducted with a straight grade Triumph flour at 50 C for 0, 1, 2, and 3 hour fermentation periods. Dough tested with 0 fermentation period was not punched. Dough tested after the 1-hour fermentation period was punched just prior to

TABLE V

GAS PRODUCTION (GP), DOUGH EXPANSION (DE), AND CALCULATED GAS LOSS (GL) IN CC OF A STRAIGHT GRADE "TRIUMPH" FLOUR, AT 50 C

Recording Time (Min)	0 Fermentation			1-Hour Fermentation			2-Hour Fermentation[1]			3-Hour Fermentation		
	GP	DE	GL	GP	DE	GL	GP	DE	GL	GP	DE	GL
0	0	0	0	0	0	0	0	0	0	0	0	0
30	25.8	22.8	3.0	35.5	31.0	4.5	32.0	30.0	2.0	36.0	29.0	7.0
60	41.3	34.4	6.9	52.0	37.5	14.5	48.0	40.0	8.0	53.0	30.2	22.8
90	53.1	37.6	15.5	64.0	39.0	25.0	51.0	40.0	11.0	61.0	30.2	30.8
120	62.7	40.5	22.2	68.0	39.0	29.0	59.0	40.0	19.0	61.5	30.2	31.3

[1]Readings for the 2-hour fermentation period were one day's test. Readings for the other fermentation periods were an average of two tests conducted on separate days.

the placement of the sample in the dough container. Dough tested after the 2-hour fermentation period was punched once at the end of this period. Dough tested after the 3-hour fermentation period was punched twice, once after 105 minutes and again after 3 hours.

With the exception of the 2-hour fermentation period, gas production increased with fermentation time during the first hour of measurements. The readings for the 2-hour fermentation period were not consistent with the other readings and no suitable explanation for this has been found. Therefore, only the 0, 1, and 3-hour fermentation periods will be considered.

The expansion of dough stopped after 60 minutes with the 3-hour fermentation time and after 90 minutes with the 1-hour fermentation time. Gas loss increased with increasing fermentation time. The steady increase in gas production and the pattern of dough expansion and gas loss were in agreement with the previously reported results (26, 28, 29, 60, 78, 86, 93, 94, 121, 127). The result of the present study suggested that the separation time of gas production and dough expansion tended to decrease with increasing fermentation time.

The rate of gas loss from doughs with 0 fermentation and with a 3-hour fermentation time was reported by Bailey and Weighley (10). They noted a difference in the rate of gas loss from doughs fermented and not fermented. In the present study, an increase in fermentation period shortened the time required for the setting of the dough. After dough expansion stopped all the gas that was produced was measured as gas loss. Thus increasing fermentation time reduced the time for stable gas loss measurements.

The Effect of Temperature on Gas Production and Retention

Tests were conducted in order to study the effects of temperature on gas production and retention. Gas production, dough expansion, and calculated gas loss after a normal 3-hour fermentation period were measured under two different temperatures. It can be seen in Table VI that gas production decreased when the temperature increased from 50 to 55 C. Dough expansion of the Kaw 61 sample was not affected by the temperature increase while it appeared that the temperature increase caused a slight decrease in the Triumph sample. High temperature might reduce enzyme activity and this could result in decreased gas production. Gas production of Kaw 61 was higher than that of Triumph at both temperatures. Temperature increase was accompanied by a decrease in gas loss in both flours. Since there was no increase in dough expansion and the increase in gas production was balanced by a corresponding increase in gas loss, after 30 minutes the dough apparently started losing all the gas produced. Consequently, the amount of gas loss measured after 30 minutes may indicate potential gas loss from a dough.

Procedure for the Determination of Gas Loss

Based on the work of previous investigators, as well as the results from the experiments conducted on the effects of air expansion, fermentation time and temperature on gas production and loss, the most suitable and reliable procedure for measuring gas loss for the other phases of this study appeared to be as follows: eight measurements were run in one day for the progeny set samples and 6 determinations were run

TABLE VI

GAS PRODUCTION (GP), DOUGH EXPANSION (DE), AND CALCULATED GAS LOSS (GL) IN CC OF STRAIGHT GRADE KAW 61 AND TRIUMPH FLOURS AT 50 C AND 55 C[1]

Recording Time (Min)	Temperature											
	50 C						55 C					
	GP		D		GL		GP		D		GL	
	Kaw 61	Triumph	Kaw 61	Triumph	Kaw 61	Triumph	Kaw 61	Triumph	Kaw 61	Triumph	Kaw 61	Triumph
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	26.0	22.5	20.5	20.0	5.5	2.5	28.0	24.5	22.5	19.5	5.5	5.0
30	41.5	36.5	26.0	29.0	15.5	7.5	39.0	32.5	24.5	23.5	14.5	9.0
45	55.0	47.0	26.0	29.5	29.0	17.5	44.5	34.0	24.5	23.5	20.0	10.5
60	63.0	54.5	26.0	30.5	37.0	24.0	46.0	34.5	24.5	23.5	21.5	11.0

[1]Average of duplicate samples tested on the same day

on the variety set samples. With this procedure it was assumed that variation due to day effects in the laboratory was confounded with the block effects in the field. The determination of gas loss was performed on duplicate samples at 55 C $\pm$ 0.5 C and temperature was controlled by use of a water bath. Eight displacement chambers, four of type 1 and four of type 2, were kept in the water bath throughout the measurement period. Type 1 displacement chambers were filled with distilled water twice after the fourth and the last run and type 2 displacement chambers were filled with distilled water at the end of the last determination each day. One hour before the measurements started, the outlets of the displacement chambers were closed by rubber stoppers and water was pushed through U-shaped outlet tube by blowing from the inlet tube. A few minutes later the pressure in the displacement chamber came to equilibrium with the atmospheric pressure. During the same period eight dough containers were kept in another water bath at 56 C. Four of these containers had a 23% KOH solution and the other four had a 23% NaCl solution (25 ml).

The formula used for the dough samples was as follows:

Flour	50 g
Yeast (active dry yeast)	0.6 g
Sugar	3.0 g
Salt	0.75 g
Shortening	1.0 g
Water	-to the required consistency

The weight of flour was corrected to a basis of 14% moisture. The yeast was made up into a suspension in lukewarm water (42.2-44.4 C) by mixing 3.0 g active dry yeast and 47 ml distilled water twice a day two

hours before the mixing of middle and last sample. The yeast suspension was stirred constantly and 10 ml was used for each sample. A stock of salt-sugar solution was prepared and used as 5.0 ml to each sample.

The flour, salt and sugar solution, shortening (Crisco) and yeast were measured into mixing bowl and required water was added to bring the resulting dough to the right consistency. The ingredients were mixed for the time which had previously been determined from the mixograph test. The dough was then taken out and placed in the fermentation cabinet at 30 C and 86% humidity. In all cases, a 3-hour fermentation period was used. The first punch was made after 105 minutes by passing the dough through the sheeter. At the end of the fermentation period the dough was punched a second time and four 10 g aliquots were placed in 50 ml glass beakers. The beakers were placed in the dough containers and the containers were placed in the water bath where the displacement chambers had been kept. Fifteen minutes later the dough containers were connected to the displacement chambers. This time was taken as zero time and the volume of the water in the receiving cylinders were recorded. The volume of the water displaced was read at 15-minute intervals for one hour.

Gas loss was measured by subtracting dough expansion from the total gas production and the average of two duplicates was recorded as the gas loss value for each sample. This method of measuring gas loss appeared to be the most reliable as discussed earlier in this chapter.

Gas Loss As a Quality Trait

In order to be a useful trait, gas loss should have sufficiently high correlation with loaf volume and other quality traits which measure

dough strength. The F values of gas loss and five other quality traits based on the variety set are shown in Table VII. The five traits, wheat and flour protein, sedimentation value, mixing time, and loaf volume are accepted as useful in breeding programs. It can be observed from this table that the F value for gas loss based on combined analysis of years and locations was significant at the 0.01 level. The other five quality traits also had F values which are significant at the 0.01 level.

However, gas loss did not have significant F values in as many comparisons as did the other five traits. Gas loss had significant F values in 7 of 12 analyses while the other traits had significant F values in at least 10 of 12 analyses. Although gas loss is apparently not as useful from a breeding standpoint as the five other quality traits with which it was compared, it could be useful in certain cases since it did not result in significant F values in certain of the analyses. Non-significant F values were probably due to experimental error in the statistical analyses of gas loss resulting from laboratory techniques involved in the measurement process. The experimental error might be reduced by improving the laboratory techniques.

Simple correlation coefficients between gas loss and five important quality traits (wheat and flour protein, sedimentation value, mixing time, and loaf volume) are shown in Table VIII. These r values are based on the variety set combined over locations, years, and years and locations. In general, the correlation coefficients between gas loss and other five quality traits were low. Correlation coefficients were significant at 0.01 level for the association of gas loss with wheat and flour protein and loaf volume. Gas loss vs. sedimentation

TABLE VII

THE F VALUES FROM ANALYSIS OF VARIANCE OF GAS LOSS AND FIVE OTHER QUALITY TRAITS BASED ON THE VARIETY SET

F Value Based on:	Trait					
	Gas Loss	Wheat Protein	Flour Protein	Sedimentation Value	Mixing Time	Loaf Volume
Cherokee 1968	1.17	16.72**	17.30**	11.55**	4.93*	22.48**
Cherokee 1969	0.41	18.66**	22.39*	31.45**	11.35**	12.37**
Goodwell 1968	4.89*	2.91	5.72**	2.22	11.48**	3.97*
Goodwell 1969	9.13**	9.73**	22.66**	18.05**	8.91**	2.97
Muskogee 1968	5.20*	1.94	1.89	2.40	1.35	3.58*
Muskogee 1969	1.15	14.68**	11.24**	19.10**	11.92**	15.58**
Combined over locations in 1968	9.14**	5.77**	7.47**	6.77**	5.45**	9.77**
Combined over locations in 1969	2.42	23.02**	34.32**	40.28**	26.93**	7.24**
Combined over years at Cherokee	1.01	31.89**	35.79**	26.07**	14.41**	26.18**
Combined over years at Goodwell	4.39**	6.91**	14.86**	5.70**	13.47**	5.60**
Combined over years at Muskogee	4.69**	5.11**	4.23**	4.76**	9.76**	7.22**
Combined over years and locations	6.53**	15.78**	19.93**	18.84**	42.07**	14.26**

*Significant at 0.05 level

**Significant at 0.01 level

TABLE VIII

SIMPLE CORRELATIONS BETWEEN GAS LOSS AND FIVE OTHER QUALITY TRAITS BASED ON THE VARIETY SET

Estimate Based on Varieties	Correlation Between				
	Gas Loss and Wheat Protein	Gas Loss and Flour Protein	Gas Loss and Sedimentation Value	Gas Loss and Mixing Time	Gas Loss and Loaf Volume
Combined over two years and three locations	-0.427^{**}_{a}	-0.324^{**}	-0.168	-0.059	-0.442^{**}
Combined over locations in 1968	-0.407^{**}_{b}	-0.361^{**}	-0.479^{**}	-0.080	-0.484^{**}
Combined over locations in 1969	-0.493^{**}_{b}	-0.494^{**}	-0.196	-0.013	-0.437^{**}
Combined over years at Cherokee	-0.234_{c}	-0.183	-0.143	-0.040	-0.160
Combined over years at Goodwell	-0.368^{*}_{c}	-0.223	-0.040	0.409^{*}	-0.435^{**}
Combined over years at Muskogee	-0.602^{**}_{c}	-0.530^{**}	-0.258	0.152	-0.446^{**}

*Significant at 0.05 level

**Significant at 0.01 level

[a]Significant values are 0.190 and 0.248 for the 0.05 and 0.01 levels respectively based on 106 degrees of freedom.

[b]Significant values are 0.268 and 0.348 for the 0.05 and 0.01 levels respectively based on 52 degrees of freedom.

[c]Significant values are 0.330 and 0.424 for the 0.05 and 0.01 levels respectively based on 34 degrees of freedom.

value and gas loss vs. mixing time did not have significant r values. Negative correlation coefficients were expected for wheat and flour protein, sedimentation value, and loaf volume. One significant positive correlation coefficient between gas loss and mixing time was obtained from the analysis based on varieties combined over the years at Goodwell.

Reported r values for simple correlations between gas retention and loaf volume were in a range of -0.36 to 0.95 (56, 63). The largest r value found in the present study was -0.484 which is lower than the majority of the r values reported by other investigators. Elling and Barmore (48) reported r values of 0.87 to 0.92 for the association between gas loss and protein content. The largest r value in the present study was -0.60. One r value for the correlation between gas loss and sedimentation value found in the present study (-0.48) was in the range of reported r values for this association (63). All r values obtained for gas loss vs. mixing time (Table VIII) were lower than those reported by Gfeller and Whiteside (58).

The low correlation between gas loss and loaf volume may be due to the time when gas loss was recorded. Some doughs may reach their maximum expansions earlier than others. Measurement on a fixed time scale may result in a low correlation.

Although most of the r values were small, they indicated a possible association of gas loss with wheat protein, flour protein, and loaf volume. In the normal evaluation of breeding lines, wheat and flour protein are determined from small samples while loaf volume tests require somewhat larger samples (1000 to 1500 g). In the present study, gas loss was measured by employing 50 g flour samples which is of the

same size sample used for protein analyses. Therefore, gas loss might be employed early in the breeding program as a quality trait so that selection for low gas loss might result in retaining lines with higher loaf volume potential.

Summary and Conclusions

In order to measure gas production and gas loss in wheat doughs, a volumetric method reported by Bailey and Johnson (9) was equipped with two modifications given by Hullett (71) and Irvin (73). A modified laboratory procedure was applied in order to determine gas loss. This trait was measured at a stage corresponding to dough proofing time at 55 C.

It was concluded that gas loss could be used as an index of gas retention. Gas loss could also be employed as a quality trait in differentiating breeding material in wheat breeding programs. It requires maximum 50 g flours for the test and might be used as an indicator of loaf volume potential. However, simple correlations between gas loss and loaf volume were not high enough to support this expectation.

Improvement of the measurement procedures for gas loss and its application to properly selected genetic material are two main areas that require further research before its acceptance as a quality trait which is useful in wheat breeding programs.

CHAPTER IV

HERITABILITY OF GAS LOSS AND VARIOUS QUALITY TRAITS

Knowledge of the heritability of important quality traits in wheat would be of value to the wheat breeder in developing varieties with improved quality characteristics. The expected response of different quality traits to selection could be compared by using heritability estimate as the criterion. Traits with high heritability would be expected to respond to rather simple selection procedures and progress for them should be relatively rapid as compared to traits with low heritability.

The majority of heritability estimates dealing with wheat quality traits have been obtained by the variance component method. This method gives heritability estimates in the broad sense. Heritability in the broad sense is defined as the ratio of the genotypic variance to the phenotypic variance (62). Reviews of the variance component method are given in the following references (32, 52, 62, 80, 81, 87, 91, 105).

A summary of the inheritance of quality characteristics in wheat was given by Hehn and Barmore (68). The heritabilities of protein content have been reported by several researchers (14, 37, 65, 87, 88, 89, 98, 100, 117, 123, 125). These heritability estimates ranged from 0.25 (125) to 0.93 (87). Worzella (134, 135) reported that the inheritance of gluten strength was governed by three major independent

genes. Heritability estimates of sedimentation value were reported by Baker et al. (14), Kaul (87), Lebsock et al. (98), Schlehuber et al. (117), and Sunderman et al. (125). These estimates ranged from 0.44 (125) to 0.90 (87). Heritability estimates of mixing time ranging from 0.60 to 0.94 have been reported by Lebsock et al. (98), Lofgreen et al. (100), and Schlehuber et al. (117). Heritability estimates of flour yield were reported by Lofgreen et al. (100) as 0.73 and 0.86 and by Schlehuber et al. (117) as 0.25. Schlehuber et al. (117) also reported heritability estimates of 0.53 for loaf volume and 0.36 for test weight. Davis et al. (37) reported heritability estimates for pearling index ranging from 0.29 to 0.60 in four different populations. Briggle et al. (25) reported heritability estimates for this trait ranging from 0.85 to 0.94. No heritability studies have been reported for gas loss.

Heritability values obtained by the variance component method may be overestimated if various genotype x year interactions are not removed. The importance of genotype x environment interaction in plant breeding has been discussed by Allard and Bradshaw (1) and Baker (13). Hypothesis and working models dealing with genotype x environment interaction have been given by Comstock and Moll (33) and Matzinger (105). Generally genotype x environment interaction is estimated from the analysis of variance in a two-way classification of genotypes and environment. This analysis gives estimates of the genotypic variance, the environmental variance and the remaining variance which is attributable to genotype x environment interaction. Bequette et al. (16), Harris et al. (64), and Finney and Fryer (53) have emphasized the importance of environmental effects on quality characteristics of wheat. Davis et al. (37) found small and inconsistent first and second order

interactions for protein content. Baker et al. (14) reported significant genotype x location and genotype x location x year interactions for sedimentation value.

The objective of this part of the study was to determine the effect of genotype and environment on gas loss and certain other quality traits by estimating their heritabilities and genotype x environment interactions, utilizing the variance component method.

Experimental Results

Estimates of phenotypic and genotypic variances and heritability for gas loss and other quality traits are presented separately for the progeny and variety sets. The results from the two sets of materials are then discussed together.

Heritability Estimates From the Progeny Set

Phenotypic and genotypic variance estimates and broad sense heritability estimates for gas loss and 11 other quality traits based on the progeny set are shown in Tables IX and X. Estimates based on individual tests of F_5 and F_6 generations were calculated under the assumption that in self-pollinated crops homozygosity is achieved to a high degree by the F_5 generation. This type of combined analysis has been previously conducted (3, 111). Estimates based on this combined analysis are shown in Table X.

The combined analysis of the F_5 and F_6 generations resulted in rather high (greater than 0.7) heritability estimates for sedimentation value, specific sedimentation, and mixing time. The heritability

TABLE IX

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE F_5 AND F_6 GENERATIONS OF THE PROGENY SET FROM INDIVIDUAL TESTS

Trait	σ^2_P		σ^2_G		H	
	F_5	F_6	F_5	F_6	F_5	F_6
Gas loss	0.9096	0.9100	0.4322	0.0000	0.475	0.000
Pearling index	4.9974	3.3894	4.3380	2.9619	0.868	0.874
Test weight	1.5209	0.2766	1.3820	0.2179	0.909	0.788
Wheat protein	0.1704	0.2510	0.0707	0.0586	0.415	0.233
Wheat ash	0.0019	0.0014	0.0009	0.0000	0.479	0.000
Flour yield	2.9263	1.7020	0.8768	0.7105	0.299	0.417
Flour protein	0.1726	0.2075	0.0927	0.0508	0.537	0.245
Flour ash	0.0006	0.0001	0.0000	0.0000	0.000	0.000
Sedimentation value	8.9122	11.730	5.7754	7.3279	0.648	0.625
Specific sedimentation	0.0818	0.0722	0.0605	0.0549	0.739	0.761
Mixing time	0.9752	0.5511	0.8260	0.4534	0.847	0.823
Mixing curve height	2.1743	0.8440	1.0377	0.0000	0.477	0.000

TABLE X

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE F_5 AND F_6 GENERATIONS OF THE PROGENY SET COMBINED OVER TWO YEARS AT ONE LOCATION

Trait	σ^2_P	σ^2_G	σ^2_{GY}	H
Gas loss	0.5543	0.1325	0.0663	0.239
Pearling index	3.0673	1.9506	1.6993**	0.636
Test weight	0.5005	0.1023	0.6977**	0.204
Wheat protein	0.1276	0.0466	0.0200	0.349
Wheat ash	0.0009	0.0000	0.0006	0.000
Flour yield	2.2199	0.8392	0.0000	0.378
Flour protein	0.1170	0.0440	0.0277	0.379
Flour ash	0.0002	0.0000	0.0000	0.136
Sedimentation value	0.0692	5.8172	0.7345	0.721
Specific sedimentation	0.0632	0.9494	0.0083	0.782
Mixing time	0.6609	0.5588	0.0809*	0.845
Mixing curve height	0.9600	0.4600	0.0096	0.479

*Significant at the 0.05 level

**Significant at the 0.01 level

estimate for gas loss was 0.24 which was slightly larger than the estimate for test weight. Heritability estimates for wheat and flour ash were nil. Wheat and flour protein, flour yield and mixing curve height had heritability estimates that were slightly greater than that for gas loss.

Estimates of heritability from the progeny set were not free from bias due to genotype x environment interactions. Although an estimate of genotype x year interaction was obtained from the combined analysis of F_5 and F_6 generations, bias due to genotype x location and genotype x location x year interactions could not be removed. Only three traits showed significant genotype x year interactions. Pearling index and test weight were significant at the 0.01 level, while mixing time was significant at the 0.05 level.

Gas loss did not show a statistically significant genotype x year interaction. Estimates of phenotypic variance for gas loss in the F_5 and F_6 generations were 0.9096 and 0.9100 respectively (Table IX). Phenotypic variance seemed to be unchanged in two generations. The magnitude of the estimated genotypic variance for gas loss was 0.4322 in the F_5 and a negative value in the F_6 generations. The negative estimate of genotypic variance was accepted as 0 for the F_6 generation test. Heritability estimates for pearling index and test weight were higher in the individual F_5 and F_6 tests (Table IX) than those obtained from the combined analysis (Table X). Heritability estimates for these two traits in the individual F_5 and F_6 tests were inflated by genotype x year interactions, since this interaction component was highly significant from the combined analysis.

Heritability Estimates From the Variety Set

Estimates of phenotypic and genotypic variances and broad sense heritabilities for 13 quality traits based on single and combined analyses of data obtained from the variety set grown at the same three locations in 1968 and 1969 are shown in Tables XI-XIX. Heritability estimates obtained from the combined analysis over two years and three locations was assumed to be the most reliable for the variety set since these estimates were relatively free of genotype x environmental interactions. This analysis revealed relatively high heritability estimates for pearling index (0.95) and test weight (0.93). Other characters with relatively high heritability estimates were specific sedimentation (0.79), sedimentation value (0.74), mixing time (0.70), and wheat ash (0.69). Gas loss had a rather low heritability estimate (0.35) which was of similar magnitude to those of wheat protein, flour yield, flour protein, mixing curve height and loaf volume. The heritability estimate for flour ash was 0.

Significant genotype x environment interactions for a number of important quality traits were observed (Table XIX). All three interaction components (GY, GL, GYL) were significant at the 0.01 level for flour protein. Genotype x location x year interactions for pearling index, test weight, flour protein, sedimentation value and specific sedimentation were significant at the 0.01 level. Wheat ash and mixing time had second order interactions which were significant at the 0.05 level. Genotype x location interactions for wheat protein, flour protein and loaf volume were significant at the 0.01 level while genotype x year

TABLE XI

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET GROWN AT CHEROKEE IN 1968 AND 1969

Trait	σ^2_P		σ^2_G		H	
	1968	1969	1968	1969	1968	1969
Gas loss	1.2213	1.3819	0.5097	0.0000	0.417	0.000
Pearling index	15.061	17.334	14.973	16.637	0.994	0.959
Test weight	1.4965	4.9079	1.4951	4.8285	0.999	0.984
Wheat protein	0.4404	0.7127	0.4141	0.6745	0.940	0.946
Wheat ash	0.0009	0.0097	0.0002	0.0082	0.281	0.844
Flour yield	0.5172	5.8676	0.4100	0.0000	0.793	0.000
Flour protein	0.4172	0.5996	0.3931	0.5728	0.942	0.955
Flour ash	0.0001	0.0003	0.0001	0.0002	0.474	0.755
Sedimentation value	48.542	97.484	44.340	94.384	0.913	0.968
Specific sedimentation	0.2350	0.5753	0.2144	0.5620	0.912	0.977
Mixing time	0.2789	2.3114	0.2224	2.1078	0.797	0.912
Mixing curve height	0.8000	1.5740	0.2333	1.3111	0.292	0.833
Loaf volume	1659.3	1994.9	1585.5	1833.6	0.955	0.919

TABLE XII

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET GROWN AT GOODWELL IN 1968 AND 1969

Trait	σ^2_P		σ^2_G		H	
	1968	1969	1968	1969	1968	1969
Gas loss	3.6873	2.7491	2.9340	2.4479	0.795	0.890
Pearling index	9.0566	8.1844	8.7249	7.6608	0.984	0.936
Test weight	0.6717	3.5385	0.6393	3.4757	0.952	0.982
Wheat protein	0.4074	0.5341	0.2673	0.4792	0.656	0.897
Wheat ash	0.0092	0.0049	0.0089	0.0035	0.965	0.716
Flour yield	0.7196	0.6953	0.6337	0.0751	0.880	0.108
Flour protein	0.5424	0.5715	0.4475	0.5463	0.825	0.956
Flour ash	0.0001	0.0004	0.0000	0.0004	0.000	0.905
Sedimentation value	10.340	10.077	5.6821	9.5194	0.549	0.944
Specific sedimentation	0.0617	0.0746	0.0403	0.0727	0.652	0.973
Mixing time	0.1187	0.4176	0.1083	0.3708	0.913	0.888
Mixing curve height	1.2777	0.8333	1.1333	0.3778	0.887	0.453
Loaf volume	1350.7	1526.6	1008.6	763.33	0.747	0.500

TABLE XIII

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET GROWN AT MUSKOGEE IN 1968 AND 1969

Trait	σ^2_P		σ^2_G		H	
	1968	1969	1968	1969	1968	1969
Gas loss	2.7741	0.4491	2.2410	0.0579	0.808	0.128
Pearling index	26.338	31.877	25.564	31.4761	0.841	0.987
Test weight	3.8296	3.9187	3.2212	3.8688	0.841	0.987
Wheat protein	0.4469	0.3445	0.2161	0.3209	0.483	0.932
Wheat ash	0.0025	0.0020	0.0022	0.0000	0.872	0.000
Flour yield	0.3274	0.3726	0.0000	0.0000	0.000	0.000
Flour protein	0.4726	0.2848	0.2238	0.2594	0.473	0.911
Flour ash	0.0001	0.0008	0.0000	0.0007	0.309	0.939
Sedimentation value	47.066	17.232	27.466	16.330	0.584	0.948
Specific sedimentation	0.1796	0.0748	0.1263	0.0713	0.703	0.954
Mixing time	0.2189	2.1289	0.0574	1.9503	0.262	0.916
Mixing curve height	2.2223	1.4556	0.0000	1.0445	0.000	0.717
Loaf volume	4208.8	2163.3	3032.5	2024.4	0.720	0.936

TABLE XIV

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET COMBINED OVER THREE LOCATIONS IN 1968

Trait	σ^2_P	σ^2_G	σ^2_{GL}	H
Gas loss	2.0286	1.7625	0.1324	0.985
Pearling index	1.0999	0.5903	2.3276**	0.537
Test weight	1.4291	1.1424	0.7836**	0.799
Wheat protein	0.2552	0.1667	0.1331	0.653
Wheat ash	0.0039	0.0009	0.0087**	0.221
Flour yield	0.2044	0.0714	0.2255*	0.349
Flour protein	0.3055	0.2196	0.1353	0.719
Flour ash	0.0000	0.0000	0.0000	0.453
Sedimentation value	21.416	14.421	11.496*	0.673
Specific sedimentation	0.1022	0.0739	0.0530*	0.723
Mixing time	0.1384	0.1048	0.0246	0.757
Mixing curve height	1.0259	0.7000	0.0000	0.682
Loaf volume	1728.2	1389.1	486.35	0.804

*Significant at the 0.05 level

**Significant at the 0.01 level

TABLE XV

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET COMBINED OVER THREE LOCATIONS IN 1969

Trait	σ^2_P	σ^2_G	σ^2_{GL}	H
Gas loss	0.5588	0.2117	0.3498	0.379
Pearling index	16.234	14.785	3.8057**	0.911
Test weight	3.4741	3.1503	0.9073**	0.907
Wheat protein	0.3104	0.1819	0.3466**	0.586
Wheat ash	0.0040	0.0034	0.0001	0.850
Flour yield	0.8376	0.0753	0.0000	0.090
Flour protein	0.2949	0.1997	0.2598**	0.677
Flour ash	0.0004	0.0004	0.0001*	0.909
Sedimentation value	20.410	9.8164	30.261**	0.481
Specific sedimentation	0.1529	0.0804	0.1549**	0.526
Mixing time	1.2840	1.1163	0.3599**	0.869
Mixing curve height	0.7205	0.2703	0.9741*	0.375
Loaf volume	608.38	0.0000	1595.9**	0.000

*Significant at the 0.01 level

**Significant at the 0.05 level

TABLE XVI

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET GROWN AT CHEROKEE COMBINED OVER TWO YEARS

Trait	σ^2_P	σ^2_G	σ^2_{GY}	H
Gas loss	0.6873	0.1639	0.0000	0.238
Pearling index	15.779	15.360	0.4446	0.973
Test weight	2.6579	2.1087	1.0530**	0.793
Wheat protein	0.5147	0.4529	0.0914*	0.879
Wheat ash	0.0032	0.0000	0.0053**	0.000
Flour yield	2.4380	0.9443	0.0000	0.387
Flour protein	0.4554	0.4024	0.0805**	0.884
Flour ash	0.0001	0.0000	0.0002*	0.000
Sedimentation value	47.446	22.147	47.214**	0.467
Specific sedimentation	0.2769	0.1489	0.2394**	0.537
Mixing time	0.9371	0.5791	0.5860**	0.618
Mixing curve height	0.8713	0.0000	1.3278**	0.000
Loaf volume	1539.3	1251.5	457.96**	0.813

*Significant at the 0.05 level

**Significant at the 0.01 level

TABLE XVII

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET GROWN AT GOODWELL COMBINED OVER TWO YEARS

Trait	$\sigma^2 P$	$\sigma^2 G$	$\sigma^2 GY$	H
Gas loss	2.0602	0.0000	3.5933**	0.000
Pearling index	7.7107	6.8009	1.3869**	0.882
Test weight	1.6004	1.0957	0.9618	0.685
Wheat protein	0.3370	0.2033	0.1699*	0.603
Wheat ash	0.0055	0.0038	0.0024*	0.702
Flour yield	0.3876	0.0679	0.2866	0.175
Flour protein	0.4460	0.3351	0.1618*	0.751
Flour ash	0.0001	0.0000	0.0002**	0.167
Sedimentation value	7.4351	4.6611	2.9397	0.627
Specific sedimentation	0.0545	0.0409	0.0155	0.749
Mixing time	0.1925	0.1169	0.1227**	0.607
Mixing curve height	1.0055	0.8555	0.0000	0.851
Loaf volume	1021.7	792.77	93.194	0.776

*Significant at the 0.05 level

**Significant at the 0.01 level

TABLE XVIII

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET GROWN AT MUSKOGEE COMBINED OVER TWO YEARS

Trait	$\sigma^2 P$	$\sigma^2 G$	$\sigma^2 GY$	H
Gas loss	1.0838	0.5560	0.5933	0.513
Pearling index	27.891	26.675	1.8450*	0.956
Test weight	3.5219	3.1698	0.3752	0.900
Wheat protein	0.3249	0.2538	0.0150	0.781
Wheat ash	0.0009	0.0000	0.0008	0.000
Flour yield	0.1869	0.0119	0.0000	0.063
Flour protein	0.2903	0.2019	0.0397	0.695
Flour Ash	0.0003	0.0000	0.0005**	0.000
Sedimentation value	24.397	16.511	5.5192	0.677
Specific sedimentation	0.0935	0.0598	0.0390	0.639
Mixing time	0.8298	0.4858	0.5181*	0.585
Mixing curve height	1.4250	0.7667	0.0000	0.538
Loaf volume	2373.6	1561.1	967.36	0.658

*Significant at the 0.05 level

**Significant at the 0.01 level

TABLE XIX

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY BASED ON THE VARIETY SET COMBINED OVER TWO YEARS AND THREE LOCATIONS

Trait	σ^2_P	σ^2_G	σ^2_{GY}	σ^2_{GL}	σ^2_{GYL}	H
Gas loss	0.8611	0.3061	0.6810**	0.0000	0.6080	0.355
Pearling index	15.759	14.948	0.0000	1.3306	1.7359**	0.948
Test weight	2.3064	2.1496	0.0000	0.0000	0.7999**	0.932
Wheat protein	0.2252	0.1094	0.0646	0.1939**	0.0275	0.485
Wheat ash	0.0025	0.0017	0.0004	0.0000	0.0023*	0.686
Flour yield	0.3109	0.1383	0.0000	0.2031	0.0000	0.445
Flour protein	0.2465	0.1326	0.0770**	0.1805**	0.0170**	0.538
Flour ash	0.0003	0.0000	0.0002**	0.0000	0.0008	0.000
Sedimentation value	17.844	13.248	0.0000	1.1915	19.687**	0.742
Specific sedimentation	0.1030	0.0824	0.0000	0.0017	0.1032**	0.799
Mixing time	0.5500	0.3864	0.2242*	0.0075	0.2158*	0.702
Mixing curve height	0.5012	0.1628	0.3222	0.1933	0.0000	0.325
Loaf volume	903.06	397.42	269.44**	804.39**	236.74	0.441

*Significant at the 0.05 level

**Significant at the 0.01 level

interactions for gas loss, flour protein, flour ash and loaf volume were significant at the 0.01 level.

Table XVII shows the estimates of variance components based on mean performance of varieties grown at Goodwell for two years. It can be observed from this table that gas loss has a 0 estimate for genotypic variance. This was apparently due to a large genotype x year interaction component in this analysis. A comparison of Tables XII and XVII further indicates that estimates of genotypic variance for gas loss based on single experiments conducted at Goodwell were inflated by the genotype x year interaction. Large estimates of heritability for gas loss were obtained from the analyses based on single experiments at Muskogee in 1968 (Table XIII), at Goodwell in 1968 and 1969 (Table XII), and combined over locations in 1968 (Table XIV). Heritability estimates for this trait based on single and combined analyses at Cherokee were somewhat lower (Tables XI and XVI). Genotype x year interaction was estimated as 0 at this location (Table XVI).

Considering traits other than gas loss, heritability estimates from single and combined analyses were consistently high for pearling index and test weight. Heritability estimates were fairly consistent for wheat protein, flour protein, sedimentation value, specific sedimentation and mixing time. Heritability estimates from single and combined analyses varied widely for wheat ash, flour ash, flour yeild, mixing curve height and loaf volume.

Discussion

The estimates of heritability for quality traits based on the two populations studied indicated that pearling index, sedimentation value,

specific sedimentation and mixing time were rather highly heritable characters. Heritability estimates of mixing time were the highest of all the heritability estimates obtained in the progeny set. The parents of the progeny set were distinctly different for mixing time as shown in Table I. This no doubt resulted in large genotypic variance estimate for mixing time in this material. Pearling index and test weight which had low estimates of heritability in the progeny set showed rather large heritability estimates in the variety set. The heritability estimate for test weight was especially high in the variety set. The parents of the progeny set were almost similar for test weight (Table I). Actual test weight values ranged from 57.1 to 61.1 in the variety set compared to ranges of from 59.2 to 60.2 in the progeny set (Tables I and II). This could result in larger genotypic variance for test weight in the variety set. Genotype x year and genotype x location interactions were also very small for test weight and pearling index in the variety set (Table XIX).

Large experimental errors associated with gas loss measurements in the laboratory and lack of genetic differences in the parents may be considered as two possible causes of these low estimates. The parents of the progeny set were very similar in gas loss characteristics (Table I). While this does not necessarily assume no differences in genes affecting this trait, the possibility exists that the progeny set did not have sufficiently high genetic variability for gas loss to show high heritability values. Undoubtedly gas loss was affected to a large degree by the environment. Genotype x year interaction for gas loss was significant at the 0.01 level in the variety set, although in the progeny set this interaction component was small and nonsignificant.

It can be observed from Tables XVI and XVIII that there was no significant genotype x year interaction for gas loss at Cherokee and Muskogee. This interaction component was significant at Goodwell (Table XVII). Any conclusions regarding the importance of environmental influence on gas loss is not possible at this time. A more extensive evaluation program for gas loss should be carried out before definite conclusions can be made.

Loaf volume tested in the variety set had a low heritability estimate in the combined analysis of years and locations (Table XIX). Heritability estimates for this quality trait were inconsistent from location to location and from year to year. In a few cases, heritability estimates for gas loss and loaf volume were in the same range (Tables XIII, XVIII and XIX). High heritability estimates for loaf volume were obtained at Cherokee for two years where gas loss had low heritability estimates.

In the present study, heritability estimates for wheat protein based on the combined analyses in the two populations were 0.35 (Table X) and 0.48 (Table XIX), while heritability estimates for flour protein of 0.38 and 0.54 were obtained in the progeny set and variety set respectively. These estimates of heritability appeared to be rather low but fell within the range of those reported by other workers (14, 37, 65, 87, 88, 89, 98, 100, 117, 123, 125). Heritability estimates as large as 0.95 for wheat protein (Table XI) and 0.96 for flour protein (Table XII) were obtained from the analyses of the single experiments in this study which would be comparable to many of those reported in the literature that were also based on single experiments at one location or for one year.

Heritability estimates for sedimentation value were larger than 0.7 in the present study. Reported heritability estimates ranged from 0.44 to 0.90 (14, 87, 98, 117, 125). One heritability estimate of 0.97 were obtained at Cherokee in 1969 (Table XI) which was larger than any reported in the literature.

Heritability estimates for mixing time were in the range of those reported by previous workers. The largest heritability estimate for mixing time in this study was 0.91 at Cherokee in 1969 (Table XI) and at Goodwell in 1968 (XII) which appeared to be close to the highest heritability estimate reported by other workers for this character (98, 100, 117).

Heritability estimates for loaf volume were generally equal to or higher than those reported from previous studies (117). Heritability estimates for test weight and pearling index were also higher than previously reported heritabilities (25, 37, 117).

Significant second order genotype x environment interactions on the major quality traits could have an important effect in the breeding programs. Sedimentation value, specific sedimentation, mixing time and flour protein should be tested and evaluated at more than one location for two or more years.

The significant genotype x location interaction for wheat protein suggested that testing for this trait at two or more locations for one year would be sufficient in a breeding program. Loaf volume had significant genotype x year and genotype x location interactions (Table XIX). Loaf volume should also be tested rather extensively at two or more locations for two or more years.

Significant genotype x environment interactions on wheat and flour

protein observed in the present study did not agree with the report by Davis et al. (37) who found no significant genotype x year interactions for this trait. Significant genotype x location x year interactions were observed for sedimentation value which is in agreement with the results reported by Baker et al. (14). The genotype x location interaction for sedimentation value was not significant in the present study although this interaction component was significant in a study reported by Baker et al. (14).

Since flour ash is related to flour yield and is affected by the milling process, little importance should be attached to heritability of this trait. It is seldom considered in a breeding program. Heritability estimates for flour yield were close to the estimates of 0.25 and 0.35 reported by Schlehuber et al. (117) and Everson and Seeborg (50).

Summary and Conclusions

Phenotypic and genotypic variances and heritabilities were estimated for gas loss and various other quality characteristics from the single and combined tests of F_5 and F_6 generations of the progeny set grown at one location for two years and from single and combined analyses of the variety set grown at three locations for two years. Genotype x environment interactions were estimated from the combined analyses in both populations. Estimates based on the combined analysis of F_5 and F_6 generations and the combined analysis of years and locations were employed as standards for the comparisons in the progeny and variety set, respectively.

Low heritability estimates of gas loss indicated that its inheritance is complex and is influenced greatly by environmental effects. Heritability estimates for gas loss were large at particular locations but these appeared to be inflated by genotype x environment interactions. Gas loss may be considered as a usable quality trait although more research is needed on laboratory measurement techniques and nature and extent of environmental influences.

It was concluded that pearling index, test weight, sedimentation value, specific sedimentation, and mixing time would present little difficulty in a breeding program due to their relatively large heritability estimates. Genetic progress for wheat and flour protein and loaf volume would be more difficult to achieve because of lower heritability estimates. Flour yield and mixing curve height had low and inconsistent heritability estimates and are of minor importance in a breeding program.

On the basis of the combined analysis of two years and three locations, the quality traits may be placed into the following genotype x environment interaction groups:

Group I: Those traits showing no significant interactions. Flour yield and mixing curve height are in this group. They might be evaluated in single experiments.

Group II: Those traits showing a significant genotype x location x year interaction. Pearling index, test weight, sedimentation value, specific sedimentation, flour protein, and mixing time are in this group. Because of the significant second order interaction, these quality traits should be tested over multiple locations and years in order to remove this interaction component from the estimates of

genotypic variance.

Group III: Those traits showing a significant genotype x location interaction. Wheat protein and loaf volume are in this group. They should be tested at multiple locations for one year in order to estimate their heritabilities.

Group IV: Those traits showing a significant genotype x year interaction. Gas loss, flour ash, and loaf volume are in this group. Heritability estimates based on two or more years at one location may be dependable for this particular set of locations in Oklahoma.

On the basis of the combined analysis of two years and three locations, gas loss and eight other important quality traits may be placed into the following heritability groups:

Group I: Those traits with high heritability estimates (> 0.90). These traits were pearling index and test weight.

Group II: Those traits with heritability estimates approximately 0.70. These traits were sedimentation value, specific sedimentation, and mixing time.

Group III: Those traits with rather low heritability estimates (0.32 to 0.54). These traits were wheat and flour protein, loaf volume and gas loss.

CHAPTER V

PHENOTYPIC AND GENOTYPIC CORRELATIONS BETWEEN QUALITY TRAITS

Phenotypic correlation has been defined as the association between two characters that can be directly observed (51). Phenotypic correlation consists of both genotypic and environmental correlations. Falconer (51) defined the genotypic correlation as the correlation of genotypic values. Knowledge of the association between important traits is of considerable importance to the plant breeder. Strong positive associations among traits for which selection is practiced would be desirable in breeding programs, while strong negative associations would present the breeder with additional difficulties.

Kaul (87) reported phenotypic and genotypic correlations between protein content and sedimentation value in a Selkirk/Gabo progeny. The phenotypic correlation coefficients were 0.058 and 0.366 in the F_1 and F_2 generations respectively. The r values for this association were very low in the F_3, F_4 and F_5 generations, ranging from -0.004 to 0.062. The genotypic correlation coefficient was 0.426 in the F_2 generation.

Baker et al. (14) reported phenotypic and genotypic correlation coefficients between percent nitrogen and sedimentation value. Both associations had an r value of 0.13. They reported that the phenotypic and genotypic correlation coefficients between percent protein and dough development time and between percent protein and tolerance index

were smaller than 0.2. Phenotypic correlation coefficients between sedimentation value and dough development time and between sedimentation value tolerance index were 0.77 and -0.65 respectively. Genotypic correlation coefficients for the same associations were 0.86 and -0.73. Phenotypic and genotypic correlation coefficients between dough development time and tolerance index were -0.91 and -0.98 respectively. In this same study thousand kernel weight showed low r values (less than 0.33) for its phenotypic and genotypic associations with the other traits.

Kaufman et al. (90) reported phenotypic correlation coefficients between percent protein and sedimentation value and between sedimentation value and dough development time with r values of -0.11 and 0.72 respectively.

Davis et al. (37) reported significant phenotypic correlation between protein content and pearling index with r values ranging from -0.11 to 0.60. The genotypic associations between these two quality traits were more inconsistent with r values ranging from 0 to 1.02.

The objective of this part of the study was to evaluate the phenotypic and genotypic associations between various wheat quality traits in order to determine their possible usefulness in breeding programs.

Experimental Results

Estimates of phenotypic and genotypic correlation coefficients for quality traits in the two populations were obtained by the variance component method. For the progeny set, correlation coefficients were estimated on a line mean basis from separate and combined analyses of the F_5 and F_6 generations. Correlation coefficients in the progeny set

were estimated for the associations of gas loss, wheat protein, sedimentation value, specific sedimentation, and mixing time with the other quality traits. For the variety set estimates of correlation coefficients were based on the mean performance of varieties combined over the two years and three locations tested. In this set, correlation coefficients of gas loss, wheat protein, sedimentation value, specific sedimentation, mixing time, and loaf volume were estimated for their associations with other quality traits. The results obtained from these two populations will be presented separately and then discussed together.

Phenotypic and Genotypic Correlations Based on the Progeny Set

Estimates of phenotypic and genotypic correlation coefficients in the progeny set are shown in Tables XX-XXIV. Correlations between gas loss and 11 quality characters as shown in Table XX indicated low or variable phenotypic and genotypic associations. Negative (favorable) phenotypic correlation coefficients between gas loss and wheat and flour protein and flour yield were significant at the 0.01 level in the F_5 generation. None of the phenotypic correlation coefficients was statistically significant in the F_6 generation. Phenotypic correlation coefficients between gas loss and flour yield and between gas loss and specific sedimentation were significant at the 0.01 and 0.05 levels respectively in the combined analysis of F_5 and F_6 generations. The signs of these significant r values were positive although they had a negative sign in the F_5 generation. Genotypic correlation coefficients between gas loss and flour protein were very high. The genotypic correlation between gas loss and flour yield had r values larger than 1 in

TABLE XX

PHENOTYPIC (P) AND GENOTYPIC (G) CORRELATIONS BETWEEN GAS LOSS AND OTHER QUALITY TRAITS IN THE PROGENY SET GROWN AT ONE LOCATION IN 1968 AND 1969

Correlation Between Gas Loss and:	Based on the F_5 Line Means, 1968		Based on the F_6 Line Means, 1969		Based on Combined 2 Year Analysis	
	P	G	P	G	P	G
Pearling index	-0.06[a]	-0.10	0.04	u	-0.05	-0.18
Test weight	0.30*	0.54	0.10	u	0.19	-0.16
Wheat protein	-0.47**	-1.22	-0.04	u	-0.26	-0.35
Wheat ash	0.13	0.20	0.10	u	-0.07	u
Flour yield	-0.37**	1.04	0.10	u	0.44**	1.331
Flour protein	-0.41**	-0.98	-0.06	u	-0.21	-0.04
Flour ash	0.30*	u[b]	-0.24	u	0.04	-0.17
Sedimentation value	-0.07	-0.22	-0.04	u	-0.04	-0.01
Specific sedimentation	-0.21	0.38	-0.09	u	0.27*	-1.21
Mixing time	-0.03	-0.11	-0.03	u	0.04	0.26
Mixing curve height	0.09	0.22	0.23	u	0.07	0.15

*Significant at the 0.05 level

**Significant at the 0.01 level

[a]Significant values for phenotypic correlations are 0.26 and 0.33 for the 0.05 and 0.01 levels respectively based on 57 degrees of freedom.

[b]u denotes undefined estimate of the correlation coefficient.

TABLE XXI

PHENOTYPIC (P) AND GENOTYPIC (G) CORRELATIONS BETWEEN WHEAT PROTEIN AND OTHER QUALITY TRAITS IN THE PROGENY SET GROWN AT ONE LOCATION IN 1968 AND 1969

Correlation Between Wheat Protein and:	Based on the F_5 Line Means, 1968		Based on the F_6 Line Means, 1969		Based on Combined 2 Year Analysis	
	P	G	P	G	P	G
Pearling index	0.09[a]	0.25	-0.22	0.10	-0.03	-0.24
Test weight	-0.34*	-0.84	-0.12	0.08	-0.09	0.78
Wheat ash	0.11	0.39	0.04	u	0.18	u
Flour yield	0.39**	0.86	-0.20	-0.69	0.38**	0.98
Flour protein	0.87**	1.27	0.96**	1.02	0.94**	1.00
Flour ash	0.07	u[b]	-0.02	u	0.01	0.42
Sedimentation value	0.15	-0.10	0.50**	0.20	0.27*	0.06
Specific sedimentation	-0.46**	-0.82	-0.05	-0.27	-0.23	-0.23
Mixing time	0.05	0.08	-0.03	0.19	0.01	-0.03
Mixing curve height	0.17	0.08	0.25	u	0.20	0.23

*Significant at the 0.05 level

**Significant at the 0.01 level

[a]Significant values for phenotypic correlations are 0.26 and 0.33 for the 0.05 and 0.01 levels respectively based on 57 degrees of freedom.

[b]u denotes undefined estimate of the correlation coefficient.

TABLE XXII

PHENOTYPIC (P) AND GENOTYPIC (G) CORRELATIONS BETWEEN SEDIMENTATION VALUE AND OTHER QUALITY TRAITS IN THE PROGENY SET GROWN AT ONE LOCATION IN 1968 AND 1969

Correlation Between Sedimentation Value and:	Based on the F_5 Line Means, 1968		Based on the F_6 Line Means, 1969		Based on Combined 2 Year Analysis	
	P	G	P	G	P	G
Pearling index	-0.04[a]	-0.06	0.19	0.32	0.09	0.15
Test weight	0.20	-0.24	-0.07	-0.01	-0.01	-0.03
Wheat ash	-0.02	-0.01	-0.06	u	-0.01	u
Flour yield	-0.21	-0.52	-0.17	-0.27	-0.16	-0.10
Flour protein	0.20	0.02	0.51**	0.19	0.28*	0.03
Flour ash	-0.26*	u[b]	-0.06	u	-0.16	-0.14
Specific sedimentation	0.75**	0.82	0.78**	0.89	0.83**	0.95
Mixing time	0.30*	0.36	0.43**	0.65	0.37**	0.39
Mixing curve height	0.09	-0.01	0.28*	u	0.24	0.45

*Significant at the 0.05 level

**Significant at the 0.01 level

[a]Significant values for phenotypic correlation are 0.26 and 0.33 for the 0.05 and 0.01 levels respectively based on 57 degrees of freedom.

[b]u denotes undefined estimate of the correlation coefficient.

TABLE XXIII

PHENOTYPIC (P) AND GENOTYPIC (G) CORRELATIONS BETWEEN SPECIFIC SEDIMENTATION AND OTHER QUALITY TRAITS IN THE PROGENY SET GROWN AT ONE LOCATION IN 1968 AND 1969

Correlation Between Specific Sedimentation and:	Based on the F_5 Line Means, 1968		Based on the F_6 Line Means, 1969		Based on Combined 2 Year Analysis	
	P	G	P	G	P	G
Pearling index	-0.07[a]	-0.10	0.17	0.43	0.12	0.27
Test weight	0.04	0.01	0.06	0.02	0.07	0.17
Wheat ash	-0.01	-0.07	0.07	u	-0.04	u
Flour yield	0.01	-0.08	-0.14	-0.17	-0.01	0.22
Flour protein	-0.49**	-0.56	-0.05	0.08	-0.27*	-0.10
Flour ash	-0.10	u[b]	-0.01	u	-0.10	-0.29
Mixing time	0.24	0.30	0.55**	0.72	0.36**	0.36
Mixing curve height	0.04	-0.13	0.10	u	0.11	0.36

*Significant at the 0.05 level

**Significant at the 0.01 level

[a]Significant values for phenotypic correlation are 0.26 and 0.33 for the 0.05 and 0.01 levels respectively based on 57 degrees of freedom.

[b]u denotes undefined estimate of the correlation coefficient.

TABLE XXIV

PHENOTYPIC (P) AND GENOTYPIC (G) CORRELATIONS BETWEEN MIXING TIME AND OTHER QUALITY TRAITS IN THE PROGENY SET GROWN AT ONE LOCATION IN 1968 AND 1969

Correlation Between Mixing Time and:	Based on the F_5 Line Means, 1968		Based on the F_6 Line Means, 1969		Based on Combined 2 Year Analysis	
	P	G	P	G	P	G
Pearling index	0.23[a]	0.27	0.27*	0.33	0.30*	0.39
Test weight	-0.37**	-0.39	-0.12	-0.15	-0.28*	-0.09
Wheat ash	0.04	0.05	0.02	u	0.11	u
Flour yield	0.12	-0.38	0.10	0.13	0.17	0.29
Flour protein	0.04	-0.01	0.09	0.31	0.01	-0.12
Flour ash	-0.08	u[b]	-0.02	u	-0.10	0.24
Mixing curve height	-0.61**	-0.82	-0.25	u	-0.50**	-0.55

*Significant at the 0.05 level

**Significant at the 0.01 level

[a]Significant values for phenotypic correlation are 0.26 and 0.33 for the 0.05 and 0.01 levels respectively based on 57 degrees of freedom.

[b]u denotes undefined estimate of the correlation coefficient.

the F_5 generation and in the combined analysis of F_5 and F_6 generations.

Correlations of wheat protein and other quality traits are shown in Table XXI. As would be expected, phenotypic correlation coefficients between wheat protein and flour protein were very high and significant at the 0.01 level in the F_5 and F_6 generations and also in the combined analysis of these two generations. Phenotypic r values between wheat protein and flour yield were significant at the 0.01 level in the F_5 generation and in the combined analysis. Wheat protein and specific sedimentation had a phenotypic correlation coefficient which was significant at the 0.01 level in the F_5 generation. Large r values for the genotypic correlation of between wheat protein and flour yield and between wheat protein and flour protein were observed (Table XXI). The genotypic correlation coefficient between wheat protein and specific sedimentation was large in the F_5 generation.

Correlation coefficients for the association of sedimentation value with the other quality traits are given in Table XXII. The phenotypic correlations of sedimentation value with specific sedimentation and mixing time had positive and significant r values. The phenotypic correlation between sedimentation value and flour yield had negative r values. The phenotypic correlation of sedimentation value with flour protein had positive r values which were significant in the F_6 generation and in the combined analysis at the 0.01 and 0.05 levels, respectively. The genotypic association between sedimentation value and specific sedimentation had large positive r values.

Phenotypic correlation coefficients between specific sedimentation and mixing time were positive and significant at the 0.05 level in the F_6 generation and in the combined 2 year analysis (Table XXIII).

Phenotypic correlation coefficients between specific sedimentation and flour protein were negative and statistically significant in the F_5 generation and in the combined analysis of two years.

Correlations of mixing time with the other quality traits are shown in Table XXIV. The phenotypic correlation of mixing time with pearling index had positive r values while its correlations with test weight and mixing curve height were all negative. Phenotypic correlation coefficients between mixing time and test weight and between mixing time and mixing curve height were statistically significant in the F_5 generation and in the combined analysis of 2 years. Genotypic correlation coefficients between mixing time and the other quality traits were low except for one rather large r value between mixing curve height in the F_5 generation (-0.82).

Phenotypic and Genotypic Correlations Based on the Variety Set

Estimates of phenotypic and genotypic correlations based on the variety set are shown in Tables XXV and XXVI. Correlation coefficients involving gas loss, wheat protein and sedimentation value with other quality traits can be observed in Table XXV. Phenotypic correlation coefficients between gas loss and test weight and between gas loss and mixing time were positive in sign and relatively large. Genotypic correlation coefficients were larger than 1 for these two associations. The phenotypic correlation between gas loss and loaf volume had an r value of -0.73. The genotypic correlation for this comparison agreed in sign and magnitude with the phenotypic correlation. Phenotypic and genotypic associations of gas loss with wheat protein, flour protein,

TABLE XXV

PHENOTYPIC (P) AND GENOTYPIC (G) CORRELATIONS BETWEEN GAS LOSS, WHEAT PROTEIN SEDIMENTATION VALUE AND OTHER QUALITY TRAITS IN THE VARIETY SET FROM THE COMBINED ANALYSIS OVER TWO YEARS AND THREE LOCATIONS

Trait	Correlation Between Gas Loss and:		Correlation Between Wheat Protein and:		Correlation Between Sedimentation Value and:	
	P	G	P	G	P	G
Pearling index	0.17[a]	0.37	-0.35	0.54	0.39	-0.37
Test weight	0.71	1.38	-0.18	-0.22	0.14	0.16
Wheat protein	-0.37	-0.11	--	--	--	--
Wheat ash	-0.14	-0.64	0.69	1.05	-0.09	-0.18
Flour yield	0.36	0.42	-0.70	-1.03	0.04	0.08
Flour protein	-0.37	-0.10	0.99**	0.98	0.47	0.35
Flour ash	-0.45	u[b]	0.44	u	-0.42	u
Sedimentation value	-0.31	-0.26	0.49	0.47	--	--
Specific sedimentation	-0.13	-0.13	0.05	0.10	0.89*	0.93
Mixing time	0.68	1.12	-0.14	-0.01	-0.05	-0.07
Mixing curve height	-0.32	-0.56	0.80	1.28	0.37	0.53
Loaf volume	-0.73	-0.92	0.73	0.94	0.41	0.21

*Significant at the 0.05 level

**Significant at the 0.01 level

[a]Significant values for phenotypic correlation are 0.81 and 0.92 for the 0.05 and 0.01 levels respectively based on 4 degrees of freedom.

[b]u denotes undefined estimate of the correlation coefficient.

TABLE XXVI

PHENOTYPIC (P) AND GENOTYPIC (G) CORRELATIONS BETWEEN SPECIFIC SEDIMENTATION, MIXING TIME, LOAF VOLUME, AND OTHER QUALITY TRAITS IN THE VARIETY SET FROM THE COMBINED ANALYSIS OVER TWO YEARS AND THREE LOCATIONS

Trait	Correlation Between Specific Sedimentation and:		Correlation Between Mixing Time and:		Correlation Between Loaf Volume and:	
	P	G	P	G	P	G
Pearling index	-0.22[a]	-0.16	0.34	0.45	0.09	0.21
Test weight	0.24	0.24	0.52	0.54	-0.64	-0.16
Wheat ash	0.49	0.50	0.27	-0.01	0.41	0.74
Flour yield	0.44	0.51	0.53	0.72	-0.33	-0.13
Flour protein	-0.02	-0.03	-0.20	-0.09	0.67	0.74
Flour ash	-0.72	u[b]	-0.21	u	0.62	u
Mixing time	0.24	-0.05	--	--	--	--
Mixing curve height	-0.07	-0.01	-0.52	-0.57	0.32	0.23
Loaf volume	0.09	-0.11	-0.17	-0.56	--	--

[a]Significant values for phenotypic correlation are 0.81 and 0.92 for the 0.05 and 0.01 levels respectively based on 4 degrees of freedom.

[b]u denotes undefined estimate of the correlation coefficient.

sedimentation value, specific sedimentation, and mixing curve height all had negative and rather small r values.

The phenotypic correlation coefficient between wheat protein and flour protein was positive and significant at the 0.01 level. Phenotypic associations of wheat protein with wheat ash, mixing curve height and loaf volume had positive and relatively large r values. Both the phenotypic and genotypic correlations between wheat protein and flour yield was negative. Wheat protein and flour protein had a very large value for their genotypic association (0.98). The genotypic correlation between wheat protein and loaf volume had an r value of 0.94.

The phenotypic correlation coefficient between sedimentation value and specific sedimentation (Table XXV) was positive and significant at the 0.01 level and a close genotypic association with an r value of 0.93 was observed for this association. The remaining associations of sedimentation value with the other quality traits had small r values.

Correlation coefficients involving specific sedimentation, mixing time, and loaf volume with other quality traits can be observed in Table XXVI. Phenotypic associations of specific sedimentation with other quality traits had small r values except for the one with flour ash which had an r value of -0.72. Genotypic correlation coefficients agreed in sign with the phenotypic r values for this trait. Phenotypic associations of mixing time with other quality traits had small r values. The genotypic correlation coefficient between mixing time and flour yield had a positive and a relatively large r value (0.72). Phenotypic correlation coefficients of loaf volume with test weight, flour protein and flour ash were relatively large. The genotypic association of loaf volume with wheat ash and flour protein had relatively

large and positive r values. The genotypic correlation coefficient between loaf volume and test weight was negative and larger than 1.

Discussion

In the progeny set, phenotypic correlations of gas loss with test weight, wheat and flour protein and flour yield had statistically significant r values but these r values were not consistent from one generation to the next. Gas loss showed no significant phenotypic correlation with any other quality traits in the variety set. This was mainly due to the magnitude of differences required for statistical significance. Coefficients as large as 0.73 for the phenotypic association gas loss and loaf volume could not be declared as significant due to the small number of degrees of freedom. The r values of phenotypic or genotypic correlations of gas loss with wheat and flour protein were negative while the phenotypic correlation coefficients between gas loss and test weight, flour yield and flour ash were positive.

In general, the genotypic correlation coefficients of gas loss with the other quality traits agreed in sign with the corresponding phenotypic association. Genotypic correlations of gas loss with wheat and flour protein had larger r values in the progeny set than in the variety set. Gas loss had a higher genotypic correlation with mixing time in the variety set than in the progeny set. Gas loss and flour protein had a strong negative genotypic association. This negative association could be employed in a breeding program. Selection for high protein content should result in low gas loss on high gas retention.

The large and significant genotypic and phenotypic correlations between wheat protein and flour protein obtained in both populations

was expected since these two traits are usually closely related. Wheat protein and flour yield also showed similar phenotypic and genotypic associations in both populations.

The magnitude of the association between sedimentation value and specific sedimentation was similar in both populations. The phenotypic association between sedimentation value and mixing time had larger r values in the variety set than in the progeny set. Specific sedimentation had closer phenotypic and genotypic association with flour protein and mixing time in the progeny set than in the variety set. Mixing time and mixing curve height showed close phenotypic and genotypic associations in the progeny set.

Johnson et al. (81) stated that genotypic correlation coefficients give an indication of a character that may be useful as an indicator for more important traits under consideration. Flour protein showed a high negative genotypic association with gas loss. Gas loss had a very high negative association with loaf volume. Wheat and flour protein had strong positive correlations. Wheat protein could be employed in a breeding program as an indicator of gas loss and loaf volume.

It should be emphasized here that the correlations observed apply only to these specific populations studied. Also, a satisfactory procedure has not been found for testing the significance of genotypic correlations. It is noted that in many cases large and variable discrepancies occurred between genotypic and phenotypic r values for the same trait. This suggests that genotypic correlations may have limited value in terms of meaningful information.

Summary and Conclusions

Phenotypic and genotypic correlation coefficients were estimated for important quality traits in two populations of hard red winter wheat. For the progeny set, correlation coefficients were estimated on the line basis from separate and combined analyses of the F_5 and F_6 generations for the associations of gas loss, wheat protein, sedimentation value, specific sedimentation and mixing time with other quality traits. For the variety set, estimates of correlation coefficients were based on the mean performance of varieties combined over the two years and three locations tested. In this set, correlation coefficients of gas loss, wheat protein, sedimentation value, specific sedimentation, mixing time and loaf volume were estimated for their associations with other quality traits.

In most comparisons, the correlation coefficients observed were not sufficiently high to indicate strong associations. Most of the correlation coefficients were inconsistent in sign and their magnitudes were small. However, certain associations were of sufficient magnitude to be of possible value in a breeding program. There were strong positive phenotypic and genotypic associations between wheat protein and flour protein and between sedimentation value and specific sedimentation in both sets of materials.

There was an indication that wheat and flour protein may be negatively correlated with gas loss. The association between these two traits, although somewhat variable, supported the general hypothesis that gas retention and protein content are correlated.

High negative phenotypic and genotypic associations between gas

loss and loaf volume obtained in the variety set supported the hypothesis that high gas retention is correlated with large loaf volume. Consequently, it appears that gas loss, if properly measured, could be used as an indicator of loaf volume.

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VITA

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