

# Genotype and Environment Effects on Wheat Quality Traits in a Population Derived from a Soft by Hard Cross

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## ABSTRACT

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Advances in understanding the biochemistry and genetics underlying wheat end-use quality require that cereal chemistry research utilize lines grown in the same environments. It also requires that effects of linkage disequilibrium and small ranges in trait variation be avoided. Our objectives were to: 1) ascertain the effects of genotype and environment and their interactions on hard and soft wheat end-use quality traits, and 2) examine relationships between traits and heritability, using recombinant inbred lines derived from a soft by hard wheat cross. All traits showed transgressive segregation. Kernel texture (KT) was not genetically correlated with mixograph traits, indicating the feasibility of producing soft-textured genotypes

with stronger mixing properties. KT was highly genetically correlated with alkaline water retention capacity (AWRC) and moderately genetically correlated with flour yield (FY). Protein content (PRO) was not genetically correlated with dough mixing time across lines, but was with dough mixing strength. KT, FY, and mixograph traits demonstrated higher heritabilities than did AWRC and PRO. Genotype and environment and their interactions affected all traits. Year caused the greatest environment effects, affecting primarily AWRC and PRO. Genotype affected mainly KT, FY, and peak time. The effect of environment on those traits supports the need to develop screening methods using genotype rather than phenotype.

Many cereal chemists strive to assist breeders in their efforts to produce lines with desirable end-use quality by identifying genetically based trait associations. Achieving success in that endeavor, however, has been hindered by several issues.

In the 1930s, the United States began to segregate wheat based on kernel texture (KT) because it affected both milling and product functionality. At that time, it was also evident that KT was affected by the environment, as was protein content (PRO), another trait influencing wheat end-use quality. Consequently, wheat became classified as "hard" or "soft" and regions of the United States were designated growing areas for hard or soft wheat. Because grain exposed to warm dry climates during the fruiting and filling periods tends to be harder in texture and has higher PRO, production of genetically harder genotypes would be reserved for the Great Plains. On the other hand, softer genotypes, lower in PRO, would be produced primarily in the areas east of the Mississippi River and in the Pacific Northwest where predominantly wet, cooler climates prevail.

That effort to segregate U.S. wheat germ plasm based on a few quality traits has likely resulted in linkage disequilibrium that has led, in some instances, to erroneous conclusions regarding cause and effect relationships between biochemical data and quality traits. For example, studies have reported softness equivalent, a measure of KT, either not correlated, moderately correlated, or strongly correlated with PRO (Gaines 1985, Finney et al 1987, Ajum and Walker 1991). Likewise, KT, holding PRO constant, has been associated with the quantity of high molecular weight glutenin subunits in some studies but not in others (Huebner and Wall 1976, Kulp 1994). Thus, correlations between traits may result merely from selection pressure having been placed on several traits.

Results from studies using too few samples have also compounded the difficulty in determining causal relationships between

traits. In such cases, correlations found may be due to chance created by the small sample size rather than pleiotropy or linked genes. A lack of correlation may result from limited trait variation in the samples studied. In addition, research on unrelated cultivars, often grown in different environments, has limited our understanding of the biochemistry and genetics underlying wheat quality. Although appropriate for studies involving fractionation and reconstitution, such samples include large confounding genetic and environmental effects. Others have reported similar concerns about the choice of samples in many wheat quality research efforts (Wrigley et al 1982, Campbell et al 1987, Lagudah et al 1988, Rousset et al 1992, Nieto-Taladriz et al 1994).

Examining traits in only a few genotypes can thus result in conclusions about trait associations that are phenotypically true for those genotypes examined but not true for wheat germ plasm at large. By choosing genotypes with high variation at the loci controlling important traits, chance trait associations can be avoided. Obviously, a study cannot include all possible genotypes, and even studying several hundred is generally not feasible. A viable and practical alternative for studying complete germ plasm sets is to study lines derived from a cross between parents with known allelic variation at the loci that control the traits of interest. Another option, when lacking knowledge of differences at the genetic level, is to choose parents that display large phenotypical differences for the traits under study. After a cross is made, lines showing trait performance outside the range of the parents are called transgressive segregates. When transgressive segregation occurs, it can be assumed that most of the possible allelic combinations at the loci affecting the traits available from the parents have been captured, and thus, offer valuable samples for identification of genetic correlations between traits.

The use of recombinant inbred lines (RILs), grown at several locations, allow for the separation of genetic and environmental effects on quality and can provide a wide range in trait values. In addition, use of RILs can also eliminate the confounding effects of linkage disequilibrium on cereal chemistry research (Burr and Burr 1991, Young 1994, Kochert 1994). Quality studies using RILs developed from hard by soft crosses have been utilized in various studies (Davis et al 1960, Sunderman et al 1965, Briggie et al 1968, Lofgren et al 1968, May et al 1989). None, however, examined both soft and hard wheat quality traits.

The present study had three main objectives: 1) to determine the amount of variation in several milling and baking quality traits resulting from the effects of genotype, environment, and genotype by environment interactions in a population derived from a soft by hard wheat cross; 2) to explore relationships between those quality traits; and 3) to examine heritability.

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## MATERIALS AND METHODS

### Development of Plant Materials

The population used in this study consisted of 78 F<sub>5</sub> derived RILs, developed by single-seed descent from a cross of NY6432-18 (NY18) and Clark's Cream (CC) (Anderson et al 1993). The soft white winter wheat NY18 was developed by Sorrells and Paterson (1986). Clark's Cream is a hard white winter wheat that displays a high level of dormancy and a moderate degree of hard wheat end-use quality. It was developed by E. G. Clark, Sedgwick, KS. The RILs, checks, and parents were grown in 1992, 1993, and 1994, in 1-m row plots, utilizing a randomized complete block design, at two locations near Ithaca, NY, with two replicates each. Planting, harvesting, and agronomic practices were appropriate for wheat grown in New York.

Growing conditions in New York in 1992 were 1–3°F cooler than normal, with a record amount of precipitation falling in July (Sorrells and Coffman 1993). In 1993, all conditions were near normal, and in 1994, temperatures were near normal while precipitation was slightly above normal (Sorrells and Neiss 1994, Sorrells 1995).

### Sample Preparation and Quality Assessment

Samples were air-aspirated and, when necessary, hand-cleaned to remove nonwheat material and shriveled kernels. They were tempered to 15% moisture and milled (Quadrumat Jr., C.W. Brabender Instruments, South Hackensack, NJ). Flour yield (FY) and softness equivalent were then determined according to Finney and Andrews (1986). KT will be used when discussing softness equivalent, with higher values indicating softer wheats. Alkaline water retention capacity (AWRC) was also determined using the Approved Method 56-10 (AACC 1995). Flour protein content (PRO) was determined using Approved Method 46-12 (AACC 1995). All values were expressed on a 14% moisture basis (mb).

### Mixograph Procedures

Dough mixing properties were measured using a 2-g mixograph (National Mfg. Div., TMC, Lincoln, NE). The computer program MIXSMART (National Mfg.) was used for mixograph data acquisition. Data were obtained from the midline curve, as that information is least sensitive to changes in the computer analysis of the parameters. Mixograph setup parameters included: 1) 6 min total run time; 2) 108 rpm mixer speed, 3) midcurve filter 2, and 4) 80 midcurve stages. Recording started as mixing was initiated.

Peak time (PT, min) was measured when the dough reached maximum resistance or minimum mobility. Percentage torque (%T) at PT was defined as peak height. The midline slope or right of peak slope (%/min) was recorded 1 min after PT and defined as overmixing slope (OSL). Overmixing peak height (OPH, %T) denotes the resistance or strength of a dough at 1 min of overmixing past PT. The curve integral (%T at the midline × 6 min) expresses the work put into mixing the dough from the start of mixing until its completion and was defined as curve area (CA). In this study, optimum water, referred to as % water absorption (WA), was first estimated utilizing the formula in Approved Method 54-40A, which predicts WA from the flour protein content (AACC 1995). That value was further refined using linear regression of KT and WA (14% mb).

Room and water temperatures were kept constant at 20°C ± 0.5 during mixogram data collection. A control flour mixogram was run before initiating sample measurement and after every 10 samples. One mixogram was run per field plot due to limited sample. Bekes et al (1994), using a 2-g mixograph, found that mixing tests resulted in coefficients of variation of ≤ 3%.

### Statistical Analysis

Descriptive statistics were determined using the Univariate procedure of SAS with the Normal option (SAS Institute, Cary, NC). For each trait, the fit to a normal distribution was checked

using the Shapiro Wilk W (SAS Institute, Cary, NC) statistic and full normal plots. When data did not fit a normal distribution, various transformations were tried to improve the normality. The only trait that was improved through transformation was PT. Thus, further analyses were conducted on log transformed values for that trait (LnPT). Homogeneity of variance for each trait across locations was evaluated using Bartlett's test (Falconer 1989). Those differences were significant for all traits, except LnPT. Consequently, a combined analysis of variance across locations was performed for each trait using weighted least squares. All factors were considered to have random effects. The sum of squares due to location, replication within location, genotype, genotype by location interactions, and experimental error were calculated from the combined analyses using the GLM procedure of SAS. The proportion of variance attributed to those sources was quantified by equating expected with actual mean squares. Although genotype by location interactions were significant for all traits, visual inspection of the graphed data indicated that those interactions were primarily due to changes in magnitude rather than in rank. Heritabilities and 95% confidence limits were calculated for each trait on an entry mean basis (Knapp et al 1985).

Least square entry means obtained from the combined analyses were compared with parental means to determine whether transgressive segregation existed for each trait. Progeny that were significantly more extreme than the nearest parent, based upon least significant difference ( $\alpha = 0.05$ ) were considered to be transgressive segregants.

Each trait was standardized within each location to adjust for variance heterogeneity before correlation analyses. The standardized variables were calculated by subtracting the mean and dividing by the root mean square error from analysis of variance within a location. Pearson product moment correlation coefficients were determined using the PROC CORR procedure of SAS. Genetic correlations ( $r_g$ ) were calculated for each pair of traits by equating expected mean cross products with actual mean cross products obtained from multivariate analysis (Falconer 1989) using the MANOVA option of the SAS GLM procedure. Partial correlation coefficients were obtained using the multiple regression module of STATISTICA (StatSoft, Tulsa, OK). All correlation analyses were conducted using data from four locations because the mixograph traits were not measured at locations one and two.

## RESULTS AND DISCUSSION

In the present study, the RILs exhibited significant transgressive segregation at both the high and the low values for all traits, except PRO (low level) and OSL (high level). That indicated a major portion of the allelic variation from the cross between NY18 and CC was captured by the 78 RILs in this population. That is, genetic recombination occurred for all the quality traits. Genetic recombination is necessary to be sure that linkage groups established within hard and soft wheats have been broken up. Transgressive segregation cannot occur unless genetic recombination has occurred (Falconer 1989). Consequently, this population is appropriate for use in uncovering trait relationships that exist due to genetics rather than chance.

### Univariate Analysis

PRO. USDA wheat quality laboratories include PRO in the battery of tests used to predict the quality potential of new lines. Functionality issues have dictated that products made from hard wheat typically require cultivars possessing relatively high PRO, due to its correlation with dough strength and leavened bread quality (Finney 1945, 1985). Many soft wheat based products require lower PRO to ensure appropriate final texture and less affinity for water, which minimizes baking time requirements (Finney 1990, Gaines et al 1996). Beginning around 1985, the soft wheat milling and baking industry voiced the concern that PRO in new cultivars was actually

verging on being too low. Thus, presently, PRO is not being considered in the decision to release new soft wheat cultivars for breeders in the eastern half of the United States.

Yearly, the historical mean range of PRO for soft wheat harvested from various locations throughout the eastern half of the United States is  $\approx 7.0$ – $11.0\%$  or higher, usually increasing toward the South. For hard wheat cultivars, mean PRO range is  $\approx 10$ – $15\%$  or higher, with hard winter wheats usually averaging  $\approx 12.0\%$  and hard spring wheats  $\approx 14.0\%$  (unpublished data).

In the present study, the population grand mean for PRO was  $10.4\%$ , and the average PRO of the lines across locations was  $7.0$ – $14.0\%$ . NY18 and CC had averages of  $9.5$  and  $10.5\%$  PRO, respectively (Fig. 1). To increase the genotypic variation for a given trait in a population, parents that display a large phenotypic difference for the trait are generally chosen. Therefore, it was surprising to find such a large range in line mean PRO obtained from parents displaying little difference in mean PRO. It suggests that they have different genes that determine PRO.

**KT.** Soft wheat product texture reportedly correlates with KT (Gaines et al 1992a,b; Faridi et al 1994). Values  $>54\%$  are considered soft textured, values of  $\approx 42$ – $53\%$  are considered semi-soft, and values  $<42\%$  are hard textured. In this study, the grand mean for KT was  $45.2\%$ , line means were  $29.7$ – $61.5\%$ . Means for NY18 and CC were  $51.7$  and  $40.7\%$ , respectively (Fig. 1). The bimodal distribution for KT suggests its variance is primarily controlled by one gene. Similar conclusions regarding the genetic control of KT have been reported (Aamodt et al 1935; Berg 1947; Symes 1965, 1969; Wrigley 1972; Mattern et al 1973; Baker 1977; Ajum and Walker 1991; Sourdille et al 1996).

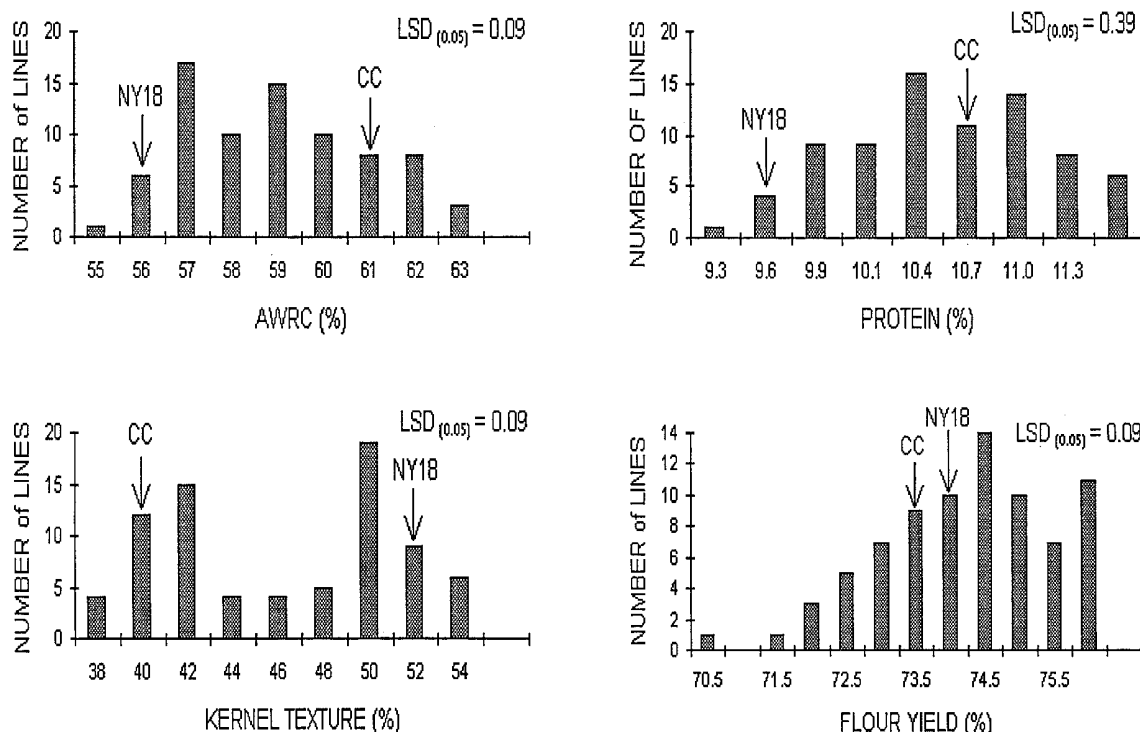
**AWRC.** The AWRC of a flour is one measure of its affinity for water. AWRC correlates reasonably well with the official AACC sugar-snap cookie spread test and with bread dough absorption (Yamazaki 1953, 1954; Gaines 1985). AWRC is a measure of flour quality used in soft wheat breeding programs. Good quality soft wheat cookie flours hold water poorly and have AWRC values of  $48$ – $55\%$ , whereas values for hard wheats generally average  $\approx 10$  percentage points higher (unpublished data).

In the present study, the overall mean across lines for AWRC was  $58.2\%$ , and the line mean values ranged from  $51.5$  to  $68.4\%$ . The mean value was  $55.7\%$  for NY18 and  $61.3\%$  for CC (Fig. 1). The variability in AWRC values was much greater in 1994 than in the previous years. After including the data from 1994, the AWRC values approached a bimodal distribution. The narrow range in values for 1992 and 1993 may have prevented this type of distribution from being clearly identified. In DNA mapping work using this same population, one marker explained much of the variation for both KT and AWRC (unpublished data). Thus, across hard and soft wheats, the variation in AWRC appears to primarily result from differences in texture. Those differences in KT then cause varying levels of damaged starch to be produced during milling, which then affects a flour's affinity for water (Greer and Stewart 1959, Meredith 1966).

**FY.** Flour yield is a measure of the straight-grade flour recovered during milling. Variation in FY likely results from inherent cultivar differences in amount of endosperm and from the interaction between aleurone cells and the innermost cells of the endosperm. Breeders use FY as an indication of how a line will perform in an industrial mill relative to other lines milled in the same manner. Genotypes with a high FY offer the milling industry added value. Across hard and soft wheat cultivars, FY range is  $\approx 70$ – $76\%$  (SWQL Quadrumat historical data) (unpublished data).

In the present study, line mean FY values for the population were  $66.9$ – $77.9\%$  with a grand mean of  $74.0\%$ . The average FY was  $74.2\%$  and  $73.8\%$  for NY18 and CC, respectively (Fig. 1). The large range in FY values for progeny derived from parents with quite similar FY values was not expected.

**Mixograph traits.** The mixograph is an instrument used to quantify various rheological attributes of wheat flour dough. The values obtained are used in some breeding programs to screen lines for dough mixing and breadbaking quality. The mixograph is also used by bakers as a guide to predict flour-mixing time, water absorption, and oxidation and enzyme requirements. There is no data available to indicate a known range in 2-g mixograph traits for soft or hard wheats because the 2-g mixograph has just recently become available and only a small number exist in the United States.



**Fig. 1.** Histogram of milling and baking quality trait values for lines derived from a cross between NY18 and CC wheat cultivars, grown in Ithaca, NY, during the 1992-1994 crop years. A line was included in a category (or represented in a bar) if its trait value was equal to or less than the number under the category down to the previous category's number.

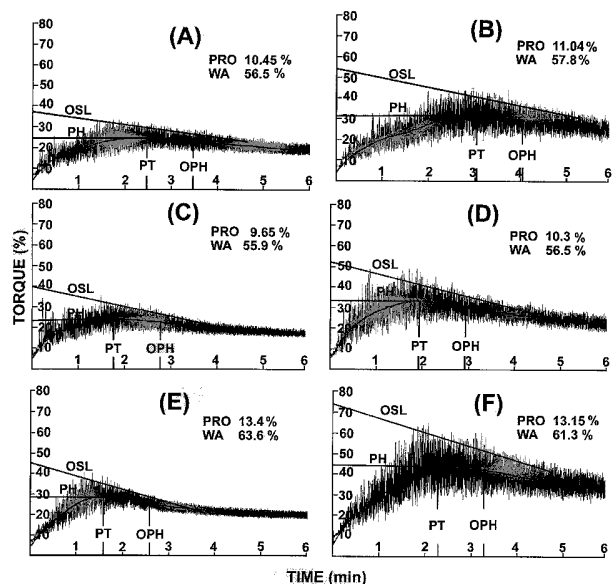
MacRitchie (1992) has suggested that at a macroscopic level, a continuous network of protein polymers is created during mixing, thus providing the dough with its characteristic viscoelastic properties. Variance in PT is reportedly related to PRO, protein quality (specific protein fractions present), and water absorption (WA) used to mix the dough (Finney and Shogren 1972). The wheat lines investigated in the present work displayed mean PT values of 1.7–3.6 min, with a grand mean of 2.4 min. The PT averages were 2.1 and 2.8 min for NY18 and CC, respectively (Fig. 2).

The peak height of a dough is the amount of torque registered by the mixograph when the dough is mixed to the point of minimum mobility and maximum extensibility. Frequently, at a comparable protein level, short (weak) and long (strong) mixing doughs register nearly equal peak height. However, longer-mixing doughs reportedly produce greater bread loaf volumes (Johnson et al 1943) that have been correlated with the quantity and quality of glutenin (Huebner and Wall 1976, Hamada et al 1982, Finney 1985, Payne 1987, Gupta et al 1992) and KT (Fowler and De La Roche 1975a). Mean values for peak height of the 78 RILs used in this study were 17.8–44.4% with a grand mean of 28.5% (Fig. 2). Mean values were 24.1 and 31.0% for NY18 and CC, respectively.

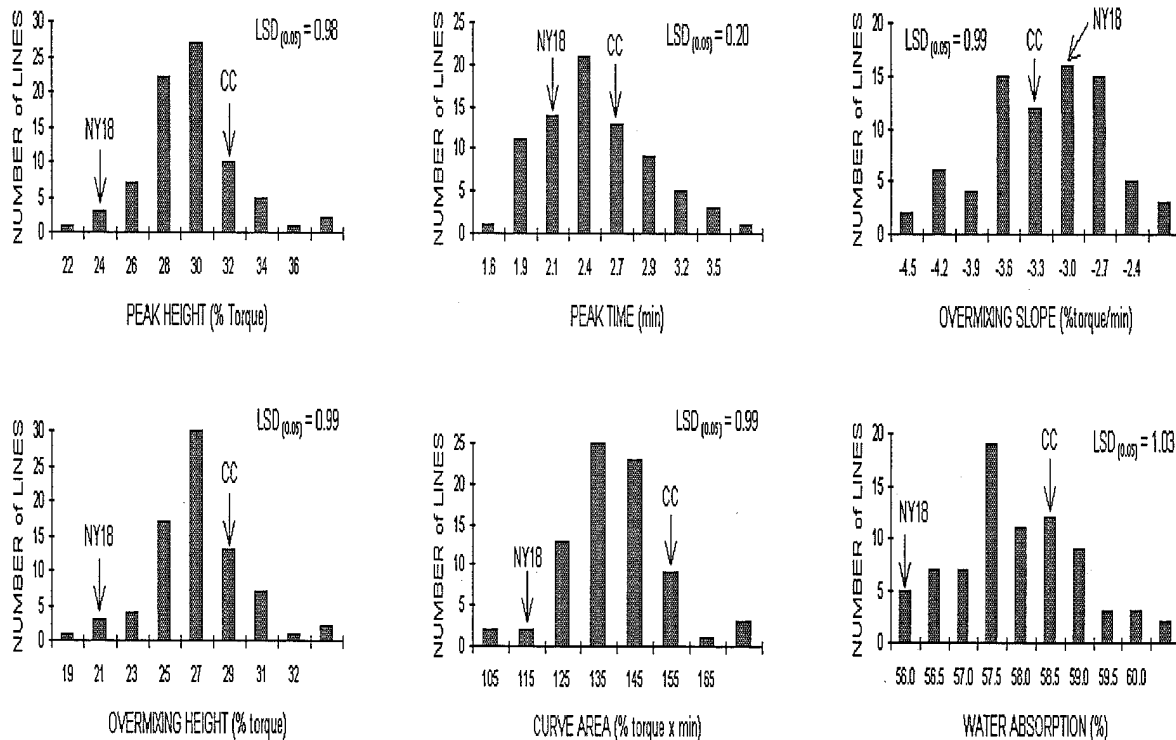
The mechanism behind dough breakdown is not completely understood. However, various theories suggest it is based primarily on the effects of oxidizing and reducing agents, compounds with activated double bonds and enzyme hydrolysis (Hoseney 1985). Information regarding flour mixing tolerance is important because poor tolerance can result in dough handling problems for both the soft and hard wheat baking industries. Mean values for overmixing slope (OSL) of the 78 RILs were 0.4 to –6.1%/min and the mean across all lines and locations was –3.3%/min (Fig. 2). The mean values were –2.9 and –3.2%/min for NY18 and CC, respectively.

In the NY18 × CC population, the RIL mean values for OPH (overmixing peak right) were 15.6–41.9%T, and the mean across lines and locations was 25.8%T (Fig. 2). The mean values were 21.7 and 28.7% for NY18 and CC, respectively (Fig. 2).

In the present study, RIL mean WA values were 56.2–60.2%. The mean values were 56.2 and 58.5% for NY18 and CC, respectively. Preliminary studies revealed the 2-g mixograph to be insensitive to differences in WA as compared to the 5-, 10-, or 35-g mixograph (data not shown). Consequently, WA was predicted for each sample based



**Fig. 3.** Mixograms of NY18 (A) and CC (B) wheat cultivars. C–F show mixograms of lines derived from the cross between A and B: a line with weaker mixing properties, ≈10% protein (C); a line with stronger mixing properties, ≈10% protein (D); a line with weaker mixing properties, ≈13% protein (E); a line with stronger mixing properties, ≈13% protein (F). All lines were grown in the same year, location, and field replication. WA = water absorption (%), PRO = flour protein content (%), PH = peak height (%T), PT = peak time (min), OSL = overmixing slope (%T/min), OPH = overmixing peak height (%T).



**Fig. 2.** Histogram of dough mixing trait values for lines derived from a cross between NY18 and CC wheat cultivars, grown in Ithaca, NY, during the 1993-1994 crop years. A line was included in a category (or represented in a bar) if its trait value was equal to or less than the number under the category down to the previous category's number.

on its PRO and KT rather than by examining the mixogram and dough consistency as recommended by Finney and Shogren (1972). The WA values here reported are a compilation of the effects of those traits.

The Mixsmart software uses the trait curve area (CA) as a summation of information for each mixogram. Mixsmart integrates the area from the top of the curve to the baseline when calculating CA. The NY18 × CC population had a CA grand mean of 134%T × min, and the line means were 82–212%T × min (Fig. 2). The mean CA values were 115 and 155%T × min for NY18 and CC, respectively.

A more meaningful numerical representation of overall dough strength might be obtained by integrating the area from the top to the bottom of the curve. Unfortunately, since Mixsmart has not been programmed to include this parameter, visual examination of mixograms will be used. Clearly, when protein levels of flours were comparable, thinner curves identify doughs with overall weaker mixing properties, whereas wider curves identify doughs with overall stronger mixing properties.

In reviews, MacRitchie (1984) and Autran (1993) have concluded that on an equal protein basis, variance in dough mixing properties is primarily explained by differences in the quantity and quality of glutenin in a flour. More specifically the *Glu-1* loci have been strongly associated with dough mixing properties, the 2+12 alleles correlate with weak mixing properties and 5+10 correlate with strong mixing properties. For PRO, NY18 and CC had mean values only 1% apart, yet respective mixograms demonstrated large differences in dough mixing strength. For example, the mixograms displayed in Fig. 3 (A and B) are examples of NY18 and CC with similar PRO. Work using polymerase chain reaction (PCR) primers developed from the *Glu-1* loci, which code for high molecular weight glutenin subunits (HMW-GS), indicates that NY18 has 2+12 alleles, whereas CC has 5+10 (unpublished data). Thus, the differences in mixing properties were not surprising. The mixograms in Fig. 3C and D were from samples of two lines containing ≈10% PRO, whereas Fig. 3E and F were from another two lines with ≈13% PRO. All four lines have subunits 2+12. Those examples demonstrate that holding PRO and the alleles at the *Glu-1D* loci constant

did not fully explain the variation in dough mixing. Differences at the other *Glu-1* loci or at loci which code for LMW-GS, gliadins, or for other biochemical components that affect dough rheology may be responsible for part of the variation in dough mixing strength.

### Analysis of Variance

The relative contributions of each source of variance to the total variance are displayed in Figs. 4 and 5. Significant effects of genotype, environment, and genotype by environment interactions were found for all traits. The variation due to environment was primarily due to year. The replication effect was low. Experimental error was also low, except for OSL and WA, which were both extremely high, probably due to the limitations of the 2-g mixograph instrument or its software.

Five of the 10 traits discussed were affected primarily by year, including AWRC, PRO, KT, OPH, and CA (Figs 4 and 5). The effect of genotype was the greatest for PT and FY, while KT and peak height were affected nearly equally by year and genotype. Bassett et al (1989) reported similar conclusions using AWRC and PRO analyses from four soft wheat cultivars grown at 21 locations for several years.

Variance due to genotype by location interactions were <10% of the total variance for all traits, except for WA (18%). Approximately equivalent variance due to genotype as for genotype by location were found for AWRC and OSL, indicating that the same genotypes either changed rank or differed in magnitude. The variance due to interaction for WA, however, resulted equally from differences in magnitude and rank. Similarly low but significant genotype by environment interactions have been reported for AWRC in soft wheats of diverse parentage (Baenziger et al 1985).

### Heritability of Traits

Heritability for all of the quality traits was high (Table I). Heritability estimates are always unique to the population under study, the growing conditions, and the experimental design used. Because all locations studied were near Ithaca, NY, and the annual growing conditions were quite similar to each other, the heritability values

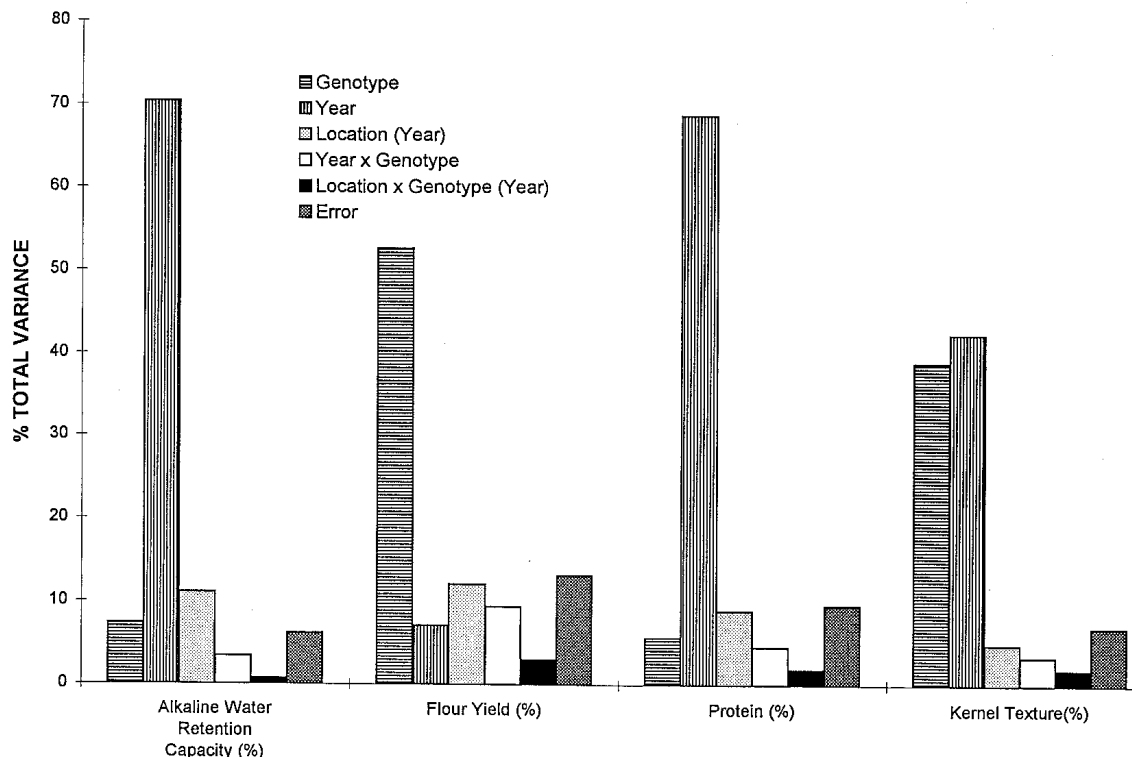


Fig. 4. Variance components for milling and baking quality traits as a percentage of total variance, on an entry mean basis for dough mixing properties determined for the NY18 × CC population, grown in Ithaca, NY, during the 1992, 1993, and 1994 crop years.

were probably elevated when compared to typical breeding populations grown over a large range of environments. Additionally, the samples were aspirated to remove diseased and shriveled kernels, thereby maximizing the quality of the lines and minimizing environmental effects. RILs also allowed for the replication of essentially homozygous lines, thus reducing the genotypic variance. Nevertheless, if those had not been issues and the heritability values had been lower, rankings would have likely remained the same. That is, KT, FY, and the mixograph traits, excluding OSL and WA, had higher heritability values than PRO, AWRC, OSL, and WA.

Reports in the literature although limited, generally are consistent with our conclusion related to trait heritability. Disagreement does exist, however, regarding FY heritability in relation to other measures of wheat quality. In a study of 15 site-year field trials, FY was only moderately heritable compared to other quality traits during several years (Fowler and De La Roche 1975b). Also, Fisher et al (1989) ranked FY heritability along with PRO, and much lower than measures of dough strength.

### Relationships Between Traits

The genetic correlation between KT and PRO was  $-0.43$  (Table II). A genetic association between those traits may be explained by work reported by Law et al (1978), who found a close linkage between the *Ha* gene and a high protein-yielding gene known as *Pro 2*. The magnitude of the correlation, however, provides a reminder that high-protein soft wheat genotypes and low-protein hard genotypes are feasible objectives for breeding programs.

The simple and genetic correlations between FY and KT were  $r = -0.54$  and  $r_g = -0.64$ , respectively (Table II). The genetic correlation between those traits is not high enough to preclude the possibility of creating high flour yielding, soft-textured genotypes. Thus, soft wheat breeders have a valuable source of alleles for greater FY in hard wheat germ plasm. Those findings are in accord with historical data from the SWQL indicating that cultivars with harder kernel texture tend to have higher FY values. Also, examining four soft wheat cultivars grown in 63 site-years, Bassett et al (1989) found FY was significantly correlated with another measurement of kernel texture ( $r = 0.72-0.81$ ).

Reports in the literature and in industrial publications document that, contrary to soft wheats, hard wheats generally have strong dough mixing properties (Kulp 1994). In the present study, KT was not genetically correlated with mixograph traits (Table II). In the United States, development of wheat cultivars with strong dough mixing properties has been a major focus for hard wheat breeding programs. Those properties have been ignored or discouraged in Western U.S. soft wheat programs (Faridi et al 1994) and ignored in Eastern U.S. soft wheat programs. Linkage disequilibrium is therefore likely to be responsible for the thinking that KT and strong dough mixing properties are genetically associated. Clarification of that issue may eventually benefit industries that produce soda (fermented) crackers, flat breads, and Chinese steamed breads, because the quality of those products would be enhanced with the availability of soft-textured grain with stronger mixing properties (Finney 1994).

The impact of PRO on peak height is apparent, because the simple and genetic correlations between those traits were  $r = 0.55$  and  $r_g = 0.70$ , respectively. Similar values were found for the correlations between PRO and CA ( $r = 0.54$  and  $r_g = 0.69$ ) and PRO and OPH ( $r = 0.52$  and  $r_g = 0.67$ ) (Table II). Higher simple correlations between PRO and mixograph traits in a group of soft wheats and a group of hard and soft wheats were reported by Morris et al (1944) and Fowler and De La Roche (1975a), respectively. Those reports and the current work demonstrate the substantial, albeit partial, role PRO plays in determining mixing properties.

The simple and genetic correlations between PT and PRO were not significant (Table II). Much evidence in the literature demonstrates that PRO is not associated with PT, neither across a population of RILs (Rousset et al 1992) nor across several cultivars grown in multiple locations (Fowler and De La Roche 1975a, Branlard et al 1991). That does not mean that PRO is not involved in causing variation in PT. For a given genotype, PT reportedly decreases as PRO increases to  $\approx 12\%$ , and thereafter, with greater PRO, PT remains constant or increases (Johnson et al 1943, Finney 1985). Because of the small number of replicates per line in the present study, correlations between PT and PRO on a line basis was not calculated. Apparently, there are factors confounding the relationship of

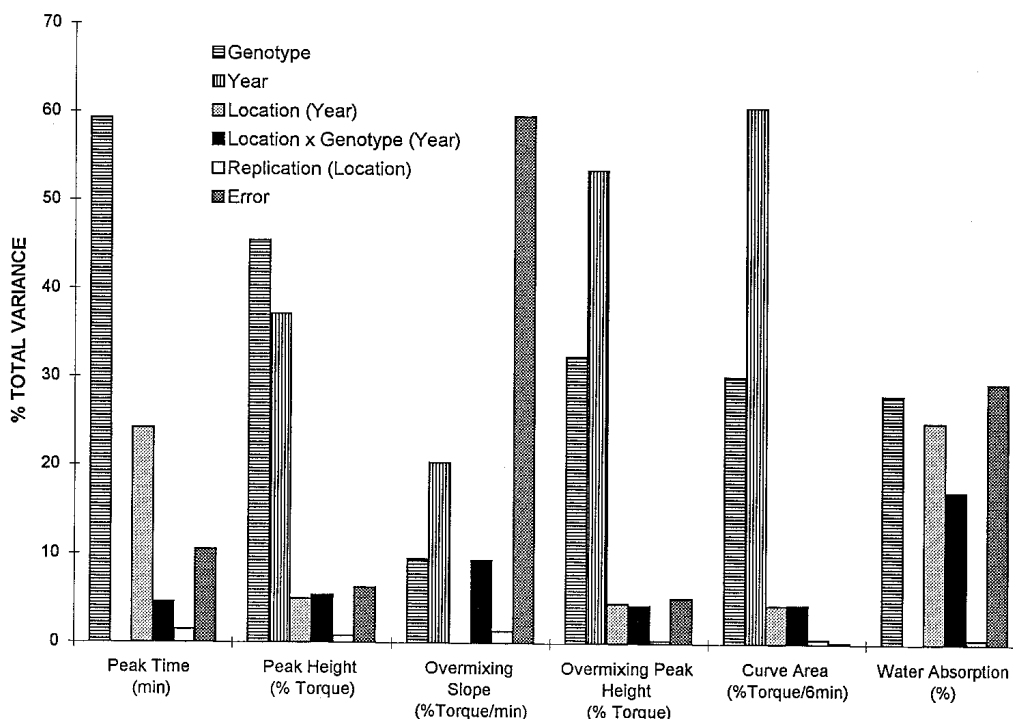


Fig. 5. Variance components for dough mixing property traits as a percentage of total variance, on an entry mean basis determined for the NY18 × CC population, grown in Ithaca, NY, during the 1993-1994 crop years.

PRO with PT, such as the ratio of glutenin to gliadin or the specific glutenin subunits or gliadins present. In short, PT is likely a function of protein quality factors and other flour biochemical constituents that affect hydration affinity, including the pentosans.

The simple and genetic correlations were moderate between peak height and OSL ( $r = -0.50$ ,  $r_g = -0.71$ ), but were high between peak height and OPH ( $r = 0.97$ ,  $r_g = 0.98$ ) and CA ( $r = 0.97$ ,  $r_g = 0.98$ ) (Table II). Others have reported varying magnitudes for inter-correlations among those traits (Fowler and De La Roche 1975a, Branlard et al 1991).

There is disagreement over how PRO and protein quality affect flour water affinity assessments, such as bread dough absorption and AWRC. Finney (1945) reported that, within hard wheat cultivars, bread dough water absorption and PRO were positively related. However, within soft wheat varieties, PRO and AWRC were only slightly correlated (Yamazaki 1954, Bassett et al 1989). The biochemical components most responsible for the variation in flour water affinity reportedly are protein quantity and quality, damaged starch, and pentosans (Bushuk 1966, Stevens 1987, Finney et al 1988, Finney 1994, Slade and Levine 1994).

In the present study, the simple and genetic correlations between AWRC and PRO were low ( $r = 0.23$  and  $r_g = 0.38$ ). Interestingly, low PRO has long been considered a requirement for consistent soft wheat product quality. Yet, AWRC, which correlates highly with sugar-snap cookie spread and is used to screen soft wheat breeders' lines, during the early generations appears to be only slightly correlated with PRO. Partial correlation analysis between PRO and AWRC, removing the effect of KT, revealed correlation coefficients of  $\approx 0$  (data not shown). Therefore, the low correlation between PRO and AWRC is likely an indirect result of the genetic

correlation (see above) between PRO and KT. Hence, PRO may not directly affect AWRC, even though its correlation with KT (and known high correlation with flour damaged starch content) makes it appear to be associated with AWRC. Also, after adjusting for PRO, AWRC was correlated with neither PT nor peak height (data not shown). Thus, it appears from this work, that protein quality also does not affect flour water affinity as measured by AWRC. Souza et al (1994), using a set of soft wheat lines with traits devoid of linkage disequilibrium, found PRO, along with a lack of the 13+19 allele of the *Glu-1B* locus, to explain 43% of the variation found for sugar-snap cookie spread. It is difficult to draw conclusions utilizing these studies due to limited descriptive information about the samples. That is, the work by Souza et al (1994) does not contain kernel texture data, and it is not known whether the different *Glu-1B* alleles were segregating in the NY18  $\times$  CC population. However, even without evidence for an association between PRO and AWRC, or between PRO and sugar-snap cookie spread, PRO does affect the texture of some products produced with soft wheat (Wade 1972, Gaines et al 1992b). Consequently, PRO remains an important trait to soft wheat end-use quality.

Conversely, in this study, KT was highly correlated with AWRC ( $r = -0.74$  and  $r_g = -0.96$ , simple and genetic correlations, respectively). The magnitude of those correlations probably resulted from the effect of KT on damaged starch production during milling. Damaged starch correlated with AWRC across hard and soft wheat cultivars and flours from coarser wheats contained more damaged starch (Jones et al 1961, Williams et al 1987). However, a significant correlation between those traits was not found in a study limited to soft wheat cultivars (Abboud et al 1985). The latter likely resulted from a limited range in damaged starch in soft wheat cultivars, which was skewed toward the low end because of decades of pressure to breed for softer KT. Thus, with limited variation in damaged starch, not only are correlations less likely but also the effect of other biochemical components, such as pentosans, may surpass the water-binding capacity of the damaged starch.

## CONCLUSIONS

This work provided evidence that soft wheat cultivars can be bred with properties targeted for specific products. For example, KT was not genetically associated with dough strength, thus the cracker industry could have access to soft wheats with strong mixing properties. That would eliminate the perceived need by many cracker bakers to composite hard and soft wheat flours from different regions of the country. Also, this study indicated that soft wheat breeders have a source of alleles associated with superior FY in hard wheat germ plasm. The effect of genotype was the greatest source of variation for KT, FY, and PT. Differences resulting from the environment were the primary source of variation for PRO and

**TABLE I**  
Milling and Baking Quality Trait Heritabilities

Trait <sup>a</sup>	Heritability	LCL <sup>b</sup>	UCL <sup>c</sup>
AWRC (%)	0.85	0.79	0.88
FY (%)	0.96	0.95	0.97
PRO (%)	0.90	0.86	0.92
KT (%)	0.98	0.98	0.99
PT (min)	0.96	0.95	0.97
PH (%T)	0.93	0.91	0.94
OSL (%T/min)	0.65	0.55	0.72
OPH (%T)	0.93	0.91	0.95
CA (%T/6 min)	0.92	0.90	0.94
WA (%)	0.83	0.78	0.87

<sup>a</sup> AWRC = alkaline water retention capacity, FY = flour yield, PRO = flour protein content, KT = kernel texture, PT = peak time, PH = peak height, OSL = overmixing slope, OPH = overmixing peak height, CA = curve area, and WA = water absorption.

<sup>b</sup> Heritability lower confidence level.

<sup>c</sup> Heritability upper confidence level.

**TABLE II**  
Genetic and Pearson Correlation Coefficients Between Wheat Quality Traits in a Population Derived from a Soft by Hard Wheat Cross <sup>a-c</sup>

	AWRC	FY	PRO	KT	PT	PH	OSL	OPH	CA	WA
AWRC (%)	1.00	0.47	0.38	-0.96	0.20	0.34	-0.12	0.38	0.30	0.94
FY (%)	0.38	1.00	0.19	-0.64	0.01	-0.10	0.15	-0.10	-0.12	0.54
PRO (%)	0.23	ns	1.00	-0.43	-0.09	0.70	-0.52	0.67	0.69	0.80
KT (%)	-0.74	-0.54	-0.33	1.00	-0.04	-0.24	0.07	-0.26	-0.20	-0.93
PT (min)	ns	ns	ns	ns	1.00	0.17	0.36	0.34	0.28	-0.02
PH (%T)	0.25	ns	0.55	-0.20	ns	1.00	-0.71	0.98	0.98	-0.02
OSL (%T/min)	ns	ns	-0.18	ns	0.21	-0.50	1.00	-0.55	-0.58	-0.27
OPH (%T)	0.26	ns	0.52	-0.20	0.16	0.97	-0.38	1.00	1.00	0.49
CA (%T/6 min)	0.24	ns	0.54	-0.16	ns	0.97	-0.37	0.98	1.00	0.46
WA (%)	0.34	0.24	0.50	-0.49	ns	0.25	ns	0.24	0.22	1.00

<sup>a</sup> Genetic correlations above the diagonal. Pearson correlations below the diagonal. AWRC = alkaline water retention capacity, FY = flour yield, PRO = flour protein content, KT = kernel texture, PT = peak time, PH = peak height, OSL = overmixing slope, OPH = overmixing peak height, CA = curve area, and WA = water absorption.

<sup>b</sup> Pearson correlations are significant at  $P < 0.001$ . ns = not significant or significant at  $P > 0.001$ .

<sup>c</sup> All correlations involving the mixograph were determined using data collected from samples grown at two New York locations during 1993 and 1994. All other correlations were determined using data collected in 1992-1994.

AWRC. Heritability was higher for most of the mixograph traits, KT, and FY than it was for PRO and AWRC. The large environmental effects on all of the traits analyzed strongly support the need to develop screening methods for quality traits using genotype rather than phenotype. Efforts to develop appropriate screening methods would necessitate close collaboration between cereal chemists and wheat geneticists.

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