Cultivar-by-Environment Interactions for Wheat Quality Traits in Semiarid Conditions

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ABSTRACT

Knowledge of the presence and magnitude of cultivar-by-environment (C × E) interactions is important to plant breeders in making decisions regarding the development and evaluation of new cultivars. In this study, 16 winter wheat cultivars were grown in 11 environments in a randomized complete block design with three replicates. The winter wheat (*Tritcum aestivum* L.) cultivars displayed a broad range of quality, and the different environments represented a broad range of environmental conditions. Test weight (TW), grain protein content (GP), sedimentation value (SED), wet gluten (WG), farinograph absorption (FAB), farinograph dough development time (FDT), quality number (FQN), resistance to extension (ER), loaf volume (LV), and baking score (BS) were measured. Highly significant differences were detected among the environments and cultivars for each of the quality variables. Significant C × E interactions indicated that the breadmaking quality evaluations must be undertaken for several environments. The WG trait showed a significant positive correlation with TW, GP, SED, LV, and BS. Path analysis indicated that GP, the most important component of quality, exhibited not only large direct effects but also large indirect ones on LV through SED, WG, FAB, and FDT. The correlation among the selected traits may be useful in future breeding programs.

When the price of wheat (*Tritcum aestivum* L.) is not formed based on quality, the respective priorities of the grower, miller, and baker are high yields of grain, flour, and bread. For the consumer, the most important aspect is bread of a high nutritive value and good organoleptic properties. However, the process starts with the cultivar's developer, the breeder, whose job is the hardest because it involves the development of a cultivar that should satisfy all the above-mentioned participants in the breadmaking process.

All living organisms have a certain relationship with their environment; this is a precondition of their survival. The success of plant breeding and production depends not only on genetic but on environmental factors as well. There are significant phenotypic differences among wheat cultivars with regard to grain and flour quality. These differences result from the action of different genes that control characters for wheat quality (Payne et al 1979). Nonetheless, environmental factors play a major role in the expression of genotype characteristics (Bassett et al 1989; Lukov and McVetty 1991; Peterson et al 1992). Their impact, however, is rarely optimal; one or more of them will always limit the yield and quality of the product. For this reason, it is very important to determine the variation of environmental factors and their effects on the processes that determine wheat quality.

The influence of environmental factors is complex and it is often not possible to determine the specific contributions of individual factors. It is estimated than ≈10% of agricultural land worldwide is not under an abiotic or biotic stress (Solh 1993). Of the areas exposed to stress, 26% is affected by drought and 15% is affected by low temperatures (Christiansen 1982). Monti (1987) estimates that drought is a limiting factor in agricultural production in as much as one third of agricultural land worldwide. Due to the global change of climate, drought is a frequent occurrence both in southern parts of central Europe and in the Balkan Peninsula, especially from 1980 onward (Jovanovic et al 1996). According to the drought index for July and August, 74% of years in Yugoslavia are either semiarid or arid. Thanks to such climatic conditions, southern Europe and southern parts of central Europe are considered suitable for the production of bread wheat (Borghi et al 1991; Bedo et al 1998; Misic and Mladenov 1998; Panayotov 1998).

Cultivar trials conducted at different sites over a number of years are the most reliable indicator of the phenotypic value of a given plant character. The purpose of such studies is to precisely measure the variation of the cultivar's mean value (Baker et al 1971) and thereby increase the possibility of finding significant differences among cultivars. Results obtained in these trials are a combination of genotype effects and environmental effects on plant development. The genotype-environment relationship is interpreted by cultivar-by-environment (C × E) interactions that mask the relationship between the genotype and phenotype and thus reduce the effects of selection (Comstock and Moll 1963). Knowing the size of the variance components associated with C × E interactions can be used in conjunction with various combinations of years, locations, and replicates to determine, through simulation, the most efficient allocation of resources for cultivar testing.

The objective of this study was to present results obtained from quality testing of replicated samples from prime winter wheat trials and to provide information of value for planning future wheat breeding programs. This investigation examined the relative contribution of the cultivar, environment, and C × E interaction to the variation observed in the qualitative characteristics of 16 winter wheat genotypes tested in 11 environments; and their inferences regarding selection and testing of new winter wheat cultivars.

MATERIALS AND METHODS

Samples

Grain samples were obtained from 16 winter wheat cultivars grown in 1995, 1996 and 1997 at several locations in Yugoslavia: Novi Sad, Indjija, Sremska Mitrovica and Kragujevac (in 1996 there was no trial at the Kragujevac site). The different environments represented a broad range of environmental conditions. These sites, located on plains, piedmont, and mountains, represent the environmental diversity of Yugoslavia (Table I). The 16 winter wheat cultivars used in the study were Sara, Novosadska rana 5, Danica, Proteinka, Novosadska rana 2, Milica, Stepa, Evropa 90, Pobeda, Kosuta, Slavija, Rusija, Jarebica, Kompas, Kragujevacka 56, Levcanka. All had diverse parentages and represented much of the current elite and historical germplasm grown in Yugoslavia. The cultivars represented a broad spectrum of baking qualities. All cultivars were agronomically suitable for production in the locations in question. The wheat cultivars were planted in a randomized complete block design with three replicates at each location. Plots of 5 m^2 with 10 rows spaced 10 cm apart were seeded at a rate of ≈230 kg/ha. Quality tests were performed on the harvested seed of each cultivar for each replicate.

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Quality Analyses

Test weight (TW) was determined using a chondrometer with a 0.25-L container (Schopper, Mehanika, Trbovlje, Slovenia). Grain protein content (GP) (N × 5.7, db) of whole meal was determined according to Kjeldahl analysis (Tecator, Höganäs, Sweden) by ICC method 105/2 (ICC 1994). Sedimentation value (SED) and wet gluten (WG) were determined according to ICC methods 116/1, and 106/2, respectively.

Wheat samples were milled on a pneumatic laboratory mill (Bühler AG, Uzwil, Switzerland) (MLU 202) after tempering to 15% moisture. Flours were tested for dough properties using a farinograph (Brabender OHG, Duisberg, Germany) according to ICC method 115/1. Farinograph absorption (FAB), farinograph dough development time (FDT), and quality number (FQN) were used in the study. FQN is a number from the table according to Hankoczy based on the planimetric area of the triangle in the farinogram. The triangle is determined by the middle of the farinographic curve as hypotenuse and the 500 BU line and line representing the softening degree of dough as the triangle's legs. Extensigram results (Brabender OHG, Duisberg, Germany) were produced using 100 g of flour according to the ICC method 114/1. Resistance to extension (ER) at the peak was measured after a rest period of 135 min. Breadmaking properties were evaluated using the standard 350-g pup loaf procedure, a straight-dough procedure with a fermentation time of 3 hr. The bake formula included flour, water, salt (2.0%), and yeast (2.0%). The loaf volume (LV) was measured by rapeseed displacement. The baking score (BS) (0–7, where 7 is excellent) was determined as a numerical expression based on the organoleptic assessment of bread crumb representing the sum of points for elasticity (0.0–4.5, where 4.5 is excellent) and pore structure fineness (0.0–2.5, 2.5 is extremely fine).

Statistical Analyses

The analysis of variance (ANOVA) and estimates of the components of variance due to cultivar (σ^2_C), cultivar by environment ($\sigma^2_{C\times E}$), and error (σ^2_e) were calculated according to Comstock and Moll (1963). Location-year combinations were treated as separate environments for statistical analyses. Both genotypes and environments were treated as random effects. Significance of mean squares for the cultivars and C × E was tested by using mean squares for C × E and pooled error, respectively. The percentage contribution of each variance component was estimated by summing the appropriate terms to give an estimate of total variance and then dividing the specific variance component by the total variance (Singh et al 1993). Ratios of variance components were calculated according to Peterson et al (1992). Coefficients of variation were determined using the formulae of Sokal and Rohlf (1987) Heritability estimates were similar to those reported by Singh et al (1993). Direct and indirect path coefficients were calculated as in Dewey and Lu (1959).

RESULTS AND DISCUSSION

Based on the pooled ANOVA, all sources of variation for each of the 10 qualitative traits were highly significant ($P < 0.01$) (Table II). In general, C × E interactions were significant ($P < 0.01$) yet relatively small. The significant C × E interaction for all quality traits resulted from the different abilities of cultivars to adjust quality to the environment as a consequence of genetic differences. For all the traits, variances due to cultivar were greater the C × E variances. These results are in agreement with the findings for semidwarf spring wheats (Lukow and McVetty 1991), soft and hard red winter wheats (Baenziger et al 1985; Peterson et al 1992), and soft white winter wheats (Bassett et al 1989). Fowler and De La Roche (1975), on

TABLE I
Coordinates, Mean Climatic Data, and Soil Classification for Each of Four Test Locations

	Novi Sad	Indjija	Sr. Mitrovica	Kragujevac
Coordinates (N)	45°33'	45°03'	45°20'	44°03'
(E)	19°85'	20°06'	19°20'	20°93'
Elevation (m)	82	136	100	190
Mean precipitation (mm)				
October-March	47.5	44.4	42.4	39.8
April-June	63.0	48.8	66.7	50.8
Mean temperature (°C)				
October-March				
Low	0.8	2.8	0.8	0.6
High	8.6	9.5	9.0	9.2
April-June				
Low	10.1	12.1	9.7	9.6
High	21.5	22.0	22.0	21.8
Soil classification[a]	Chernozem Chernic	Chernozem Calcic	Chernozem Gleyic	Vertisols Eutric

[a] World reference base for soil resources, FAO, Rome, 1998.

TABLE II
Mean Squares for Analysis of Variance Across Environments in the 1995-1997 Growing Seasons

Source of Variation[a]	df	Quality Traits[b]									
		TW	GP	SED	WG	FAB	FDT	FQN	ER	LV	BS
Environment (E)	10	272.68**[c]	71.52**	2,060.9**	948.04**	31.70**	7,062.3**	2,376.3**	190,206**	558,182**	12.22**
Rep.	22	0.29	0.11	5.9	0.26	5.39	23.6	13.9	205	720	0.04
Cultivar (C)	15	16.33**	6.21**	561.8**	116.70**	88.04**	3,203.8**	1,066.9**	487,910**	327,404**	30.97**
C × E	150	2.95**	0.87**	44.8**	11.12***	5.50**	683.2**	2,54.7**	17,735**	24,293**	2.95**
Pooled error	330	0.04	0.01	1.0	0.02	0.61	14.0	4.1	18	110	0.01
σ^2_C		28.6	35.2	50.1	46.2	52.8	24.4	21.9	70.6	52.9	46.2
$\sigma^2_{C\times E}$		68.6	61.8	46.6	53.4	34.4	71.2	74.4	29.3	46.4	53.3
σ^2_e		2.8	3.0	3.3	0.3	12.8	4.5	3.7	0.1	0.6	0.5
$\sigma^2_C/\sigma^2_{C\times E}$		0.4	0.6	1.1	0.9	1.5	0.3	0.3	2.4	1.1	0.9
^{2}		0.29	0.35	0.50	0.46	0.53	0.24	0.22	0.71	0.53	0.46

[a] % Total variance for each source of variation (σ^2_C; $\sigma^2_{C\times E}$; σ^2_e), ratios of variances estimated for cultivar main effect and interaction ($\sigma^2_C/\sigma^2_{C\times E}$) and heritability ($H^2$) of 10 quality traits.

[b] TW = test weight, GP = grain protein contents, SED = sedimentation values, WG = wet gluten, FAB = farinograph absorption, FDT = farinograph dough development time, FQN = quality number, ER = resistance to extension, LV = loaf volume, BS = baking score.

[c] ** = Significant at $P < 0.01$.

the other hand, reported relatively insignificant C × E interactions for the qualitative traits of hard red spring wheat. The environmental range used by these authors was apparently quite narrow, reducing the likelihood of significant C × E interactions.

Components of variance for each qualitative trait expressed as percentage illustrate the relative contribution of each source to total variance (Table II). The variance component due to cultivar explained most of the total variation, ranging from 21.9 to 70.6% of the variability associated with each quality parameter. Effects of C × E interaction ranged from a low of 29.3% of total variance for ER to a high of 74.4% of total variance for FQN. The relatively large C × E interactions for TW, GP, WG, FDT, FQN, and BS require multiple year and site testing to accurately assess the genetic potential. The results of this study for TW (large environmental and small cultivar effects) show that this trait can be used in the breeding process as a reliable indicator of the cultivar's biological plasticity and its adaptability to different environmental conditions (Fowler and De La Roche 1975) as well as a criterion of its resistance to air drought and high air temperatures at grain fill (Misic and Mladenov 1998).

The importance of the C × E interaction in relation to genetic effects can be shown through the ratio of the variance component $\sigma^2_C/\sigma^2_{C\times E}$ (Table II). The ratio of cultivar to C × E effects differed among the quality parameters measured. A ratio >1.0 indicates greater influence and stability of genetic factors relative to the variability associated with the interaction of C × E (Peterson et al 1992). The ratios for all the qualitative traits ranged from 0.3 to 2.4. The ratios for ER (2.4) and FAB (1.5) showed a larger influence on variability by the cultivar than the C × E interaction. The ratios for TW (0.4), GP (0.6), FDT (0.3), and FQN (0.3) were all <1.0, indicating the important influence of the C × E interaction on these qualitative traits. Variances associated with the C × E interaction were of similar magnitude as genetic components for SED, WG, LV, and BS. Grain quality is a complex character that depends on a number of traits, and the individual contribution of each traits varies depending on the specific reaction to environmental conditions. For an effective selection for a particular trait, it is important to define the conditions of its maximum phenotypic expression.

The relative magnitude of the variance components indicated that the interaction of C × E was of considerable importance in determining wheat quality. Large variance components for C × E interactions are not unexpected in studies involving a large geographic area and genotypes selected at different sites within and outside the region studied. The significant cultivar variance component indicated that the cultivars differed in their genetic potential for quality.

A wide range for all quality parameters was observed (Table III). Ranges in TW, GP, and WG across environments were notably larger than those established across cultivars. Ranges in SED and FDT were similar for cultivars and environments. Ranges in FAB, QN, ER, LV, and BS across cultivar were notably larger than those established across environments. Wide ranges in most of the qualitative traits were not unexpected because of the large differences among cultivars, test sites for available soil, and climatic data.

There was a significant C × E interaction for all the quality traits studied. The information on different types of C × E interaction is necessary when allocating the materials and analyzing the influence of locations and years. This means that the evaluation of breeding lines over several environments will give a more accurate estimate of their quality potential. The relatively large contributions (>20%) (Lukow and McVetty 1991) of cultivar variance and C × E interactions for some traits (TW, GP, FDT, FQN) also suggest that these quality parameters may require multiple environment testing to accurately assess the genetic potential of wheat lines. Cultivars are usually evaluated for at least three successive years. In the present study, although the C × E interaction effect was significant for all the quantitative traits, it was lower in magnitude than the cultivar effects. The effect of environments was confusing in the estimates obtained (Table II), therefore it is not possible to comment on the optimum number of years and sites desirable for quality testing. Bhatt and Derera (1975) argue that it is better to test over a number of sites in a few years than over a number of years in a few sites. Bassett et al (1989), on the other hand, emphasize that seasonal effects are usually greater than site effects.

Heritability is a measure of the ability of the plant breeder to recognize genetic differences among cultivars. Genetic variance indicates the potential for improvement in a population (Baker et al 1971). Given a population from which to select, successful selection is dependent on high heritability. Heritabilities for all quality parameters are presented in Table II. The heritability estimates were 0.22–0.71. It is evident from Table II that the heritability for ER was high. The traits SED, WG, FAB, LV, and BS indicated moderate heritabilities. The heritability of the traits TW, GP, FDT, and FQN was low, which is due to the large C × E interaction. Fowler and De La Roche (1975) and Bhatt and Derera (1975) also reported moderate to low values of heritability for qualitative traits in wheat. That heritability estimates for certain qualitative traits are usually lower than those for the other agronomic traits in wheat suggests that environmental effects constitute a major portion of the total phenotypic variation of these traits.

Knowing the dependence of technological quality on its various components and the interdependence of bread quality components is a major prerequisite for a successful application of proper selection methods in breeding for high technological quality of bread. Correlations between the traits depend on genetic and environmental factors. Pleiotropic gene effects and gene linkage are the main reasons for the existence of genetic correlations between traits (Falconer and Mackay 1996). When several traits are involved in evaluation of quality, it is desirable to determine correlations among them. In the present study, 45 possible pairs of traits were examined for interrelationships. The correlations among the various traits are presented in Table IV. SED and FQN were positively and, in some cases, significantly correlated with the other indicators of technolo-

TABLE III

Cultivar and Environment Mean Values for 10 Quality Traits of 16 Bread Wheats Grown in 11 Environments in 1995-97

Trait	Range				Mean (n = 176)	CV (%)
	Cultivar (n = 16)	CV (%)	Environment (n = 11)	CV (%)		
Test weight (kg/hL)	78.6–81.3	0.9	76.2–83.7	3.0	79.7	3.2
Grain protein content (%)	12.0–13.6	3.4	10.9–15.5	9.7	12.6	10.6
Sedimentation value (mL)	25.9–43.7	11.3	27.1–45.2	18.0	36.5	22.6
Wet gluten (%)	26.3–32.3	6.4	22.9–35.1	15.1	29.5	16.8
Farinograph absorption (%)	54.5–60.6	2.9	55.4–58.0	1.4	56.6	3.8
Farinograph dough development time (min)	2.5–6.8	29.1	2.1–6.8	36.3	4.3	61.3
Quality number (BU)	47.5–71.1	8.9	50.4–71.4	11.1	63.6	19.1
Resistance to extension (BU)	198.2–658.2	27.6	331.9–533.1	14.3	441.0	34.1
Loaf volume (mL)	1,110–1,486	8.0	1,132–1,441	8.7	1,244	13.2
Baking score (0–7)	3.6–6.7	20.0	4.0–5.6	10.4	4.8	28.9

TABLE IV
Correlations Among 10 Quality Traits[a] in Bread Wheat Cultivars from Yugoslavia

	GP	SED	WG	FAB	FDT	FQN	ER	LV	BS
TW	0.49*[b]	0.25	0.43*	0.59**	0.23	0.04	–0.28	0.46*	0.49*
GP		0.28	0.79**	0.45*	0.33	0.07	–0.20	0.79**	0.60**
SED			0.49*	0.22	0.23	0.66**	0.57*	0.29	0.46*
WG				0.36	0.17	0.02	–0.06	0.59*	0.54*
FAB					0.47*	0.09	–0.55*	0.51*	0.55*
FDT						0.61**	–0.36	0.49*	0.51*
FQN							0.38	0.08	0.20
ER								–0.18	0.11
LV									0.90**

[a] TW = test weight, GP = grain protein contents, SED = sedimentation values, WG = wet gluten, FAB = farinograph absorption, FDT = farinograph dough development time, FQN = quality number, ER = resistance to extension, LV = loaf volume, BS = baking score.
[b] *, ** = Significant at $P < 0.05$ and 0.01, respectively.

TABLE V
Direct and Indirect Effects on Loaf Volume (LV) from Grain Protein Contents (GP), Sedimentation Values (SED), Wet Gluten (WG), Farinograph Absorption (FAB), and Farinograph Dough Development Time (FDP) in Bread Wheat from Yugoslavia

		Indirect Effect on LV				
Component	Direct Effect on LV	GP	SED	WG	FAB	FDP
GP	0.73*[a]	· · ·	0.02	–0.08	0.06	0.06
SED	0.06	0.21	· · ·	–0.05	0.03	0.04
WG	–0.10	0.58	0.03	· · ·	0.05	0.03
FAB	0.12	0.33	0.01	–0.04	· · ·	0.09
FDP	0.19	0.24	0.02	–0.02	0.06	· · ·

[a] * = Significant at $P < 0.05$.

gical quality. ER correlated negatively with FAB and positively with SED. The trait WG showed significant positive correlation with TW, GP, SED, LV, and BS. The baking test traits, BS and LV, were positively correlated and also showed significant positive correlation with TW, GP, SED, FAB, and FDT but were not significantly correlated with FQN and ER.

The high positive correlation between BS and LV that was established in our study is in close agreement with that reported by Bhatt and Derera (1975) and Dong et al (1992). Accordingly, LV was in a higher correlation with GP and WG than BS was, and because LV was more heritable than BS, LV should be preferred as a trait in quality assessment. According to Falconer and Mackay (1996), when two traits are highly correlated and a choice must be made between them, the one with the higher heritability should be the preferred measurement. BS may be looked upon as a relatively nonmathematical selection index to facilitate consideration of the overall baking quality of the breeding material, although BS is a partially subjective assessment and one based on scoring of other quality traits related to baking. Bhatt and Derera (1975) also suggested that assessment in terms of BS must be done in addition to measuring LV.

The correlations were analyzed further by the path-coefficient approach, which involves partitioning the correlation coefficients into direct and indirect effects by alternative traits or pathways. LV, being the complex outcome of different traits and the best estimate of bread wheat baking quality, was considered to be the resultant variable, while GP, SED, WG, FAB, and FDT were the causal variables. This analysis gives a somewhat different picture than the correlation analysis. The direct and indirect effects of the seven quality traits are shown in Table V. GP, SED, FAB, and FDT showed positive and WG nonsignificant direct effects on LV. Path analysis again identified GP (0.73) as the most important quality component, as it had a large positive direct effect on LV. The positive correlation between SED, FAB, FDT and LV was mainly due to the positive indirect effect of SED, FAB and FDT by GP.

The significant positive correlations among GP, FAB, FDT, LV, and BS are in agreement with the findings of most other researchers (Baker et al 1971; Bhatt and Derera 1975; Dong et al 1992). Parameters obtained on a farinograph serve as the bases for the selection of procedures in the dough processing, fermentation, and baking stages. FAB is generally considered to be an important factor in LV (Baker et al 1971), and its failure to appear in the prediction is somewhat confusing. Direct effects of FAB and FDT are insignificant, confirming that the importance of farinograph for LV is small.

In the early generations, it is economically unjustified to select for a large number of qualitative characteristics. The results of our study confirm that grain protein content can be a breeding criterion in the early generations. However, indirect selection for a character as complex as technological quality is pregnant with risks. As relative indicators of the quantitative agreement between two variables, correlations suggest the directions of the selection-induced changes of character means. A drastic increase in one component of technological quality causes compensatory changes in the others. Because of this, relationships among characters should be changed slowly and gradually. The improvement of one trait can improve or disrupt the values of the others. This is why, in the older generations of cultivar development, comparative consideration of a number of indicators of technological quality is of particular importance. Only cultivars with well-balanced and stable indicators of quality can defy the unfavorable conditions of growing.

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