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Genetic improvement trends in agronomic performances and end-use quality characteristics among hard red winter wheat cultivars in Nebraska

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Abstract
Evaluation of wheat cultivars from different eras allows breeders to determine changes in agronomic and end-use quality characteristics associated with grain yield and end-use quality improvement over time. The objective of this research was to examine the trends in agronomic and end-use quality characteristics of hard red winter wheat cultivars grown in Nebraska. Thirty historically important and popular hard red winter wheat cultivars introduced or released between 1874 and 2000 were evaluated at Lincoln, Mead, and North Platte, Nebraska in 2002 and 2003. An alpha lattice design with 15 incomplete blocks of two plots and three replications was used at all locations. Agronomic (days to flowering, plant height, spike length, culm length, grain yield and yield components, and grain volume weight) and end-use quality (flour yield, SDS-sedimentation value, flour protein content, and mixograph time and tolerance) traits were measured in each environment. Highly significant differences were observed among environments, genotypes and their interactions for most agronomic and end-use quality characteristics. Unlike modern cultivars, older cultivars were low yielding, and less responsive to favorable environments for grain yield and yield components. Semidwarf cultivars were more stable for plant height than traditional medium to tall cultivars. All cultivars had high grain volume weight since it is part of the grading system and highly selected for in cultivar release. Modern cultivars were less stable than older cultivars for SDS-sedimentation and mixing tolerance. However, the stability of older cultivars was attributed to their having weak mixing tolerance and reduced SDS-sedimentation values. The reduced protein content of modern cultivars was offset by increased functionality, as measured by mixograph and SDS sedimentation. In conclusion, breeders have tailored agronomic and end-use quality traits essential for hard red winter wheat production and marketing in Nebraska.

Keywords: bread wheat, genetic gain, grain yield, GXE, *Triticum aestivum*

Hard red winter wheat (*Triticum aestivum* L.) is the largest wheat class produced and exported from the United States. It is mainly produced in the Great Plains for grain, though in the Southern Great Plains, it is often grazed as forage prior to stem elongation (Khalil *et al.*, 2002a). Though there is decreasing hectarage, the average production and yield of winter wheat has consistently increased in the U.S. From 1909 to 2003, the average winter wheat yield in Nebraska increased sixfold from 0.5 to 3.2 tons per ha (NASS, 2003) due to cultivars with improved agronomic characters and appropriate management practices (Cox *et al.*, 1986; Baenziger *et al.*, 2001).

The merits of genetic improvement and its cost necessitate periodical evaluation of its benefits. This evaluation is useful both to demonstrate the importance of plant breeding and as way of identifying traits or target environments that may require increased efforts by breeders (Cox *et al.*, 1988). Furthermore, genetic gain assessment is vital for evaluating selection efficiency and identifying associated traits as criteria for future selection.

Various approaches have been used to estimate genetic gain in agronomic and end-use quality characteristics in wheat. For example, progress has been evaluated from the differences between historic check cultivars and the mean yield of highest yielding lines from multi-environment cultivar trial data. Schmidt & Worrall (1984) estimated genetic gain as the grain yield of the highest yielding lines in regional breeders' nurseries as percentages of long-term checks from 3-year means. They found 0.75% and 1.5% increase per year in grain yield from 1960 to 1980 in the hard red winter wheat Northern and Southern Regional Performance Nurseries, respectively. Feyerherm *et al.* (1984), who used differential yielding ability computed as the differences between high yielding cultivars and the check cultivars, reported up to 31% yield advantage of the top five entries over the long-standing checks in a Great Plains hard red winter wheat nursery from 1920 to 1979. Genetic gain estimated from the difference between checks and top-yielding cultivars are biased by the genotype by environment interactions (GEIs), especially where crossover interactions occur and older cultivars are grown under modern cultural practices. Studies of genetic gain that use check cultivars depend on the assumption of non-significant GEI involving the checks and other cultivars to avoid confounding environmental effects (Cox *et al.*, 1988). They recommended evaluation of cultivars from different eras in common environments to evaluate the genetic gain. Using regression analysis, the genetic gain of grain yield was 0–1.4% in 38 hard red winter wheat cultivars released from 1874 to 1987 in Kansas (Cox *et al.*, 1988) and 0.2% in 12 cultivars from 1969 to 1993 in Oklahoma (Khalil *et al.*, 1995). Donmez *et al.* (2001) reported mean genetic gains of 0.15% (for cultivars released in the 1940s compared to "Turkey" which was listed as being released in 1873, though its release date has also been reported as 1874—Cox *et al.*, 1989) and 0.63% (for cultivars released in the mid to late 1990s compared to Turkey) per year for 12 hard red winter wheat genotypes in Kansas.

Estimates of genetic gain also can identify the underlying causes of yield improvement and be used to design indirect selection strategies (Morrison *et al.*, 2000). The increase in grain yield was largely associated with the improvement of harvest index and lodging resistance with only small changes in total dry matter weight of crops (Slafer & Andrade, 1989; Bell *et al.*, 1995). The harvest index increase, resulting mainly from larger numbers of kernels per square meter (Calderini *et al.*, 1995; Sayre *et al.*, 1997) was obtained by combining genes for reduced height and resistance to lodging, diseases, insects, and environmental stresses. Modern wheat cultivars tend to be shorter, earlier flowering and produce more tillers than their ancestors (Austin *et al.*, 1989).

Hard red winter wheat is primarily used to produce yeast-leavened bread (Smith, 1995) and cultivars have been selected for high milling and baking potential. Grain characteristics used as indicators of milling quality include grain volume weight, kernel weight, and flour yield; whereas indicators of baking quality include wheat or flour protein content, Mixograph mixing time, Mixograph mixing tolerance, water absorption, loaf volume and crumb grain and color (Finney *et al.*, 1987). As with agronomic characteristics, end-use quality characteristics of a wheat genotype will vary with the environment (Peterson *et al.*, 1992). Hence estimates of genetic gain must be from multiple environments.

Despite their importance, studies on the genetic gain in agronomic and end-use quality traits of hard red winter wheat have not been done in Nebraska using designed experiments. End-use quality genetic gain estimates are important to investigate if improvements in grain yield affected end-use quality (Cox *et al.*, 1989). Wheat breeders try to select lines responsive to favorable environments for grain yield and yield components, with consistent or stable performance for end-use quality. The objectives of this study were to 1) measure in Nebraska agronomic performance and end-use quality characteristics of thirty hard red winter wheat cultivars released from 1874 to 2000 and 2) examine the phenotypic stability and the genetic gains in agronomic and end-use quality characteristics among the same cultivars.

Materials and methods

Plant materials

Thirty hard red winter wheat cultivars, introduced or released between 1874 and 2000, were used in this study (Table 1). Information about each cultivar was obtained from the Germplasm Resource Information Network (GRIN) website (http://www.ars-grin.gov). The cultivars were carefully selected to represent many historically important and currently widely grown hard red winter wheat cultivars in Nebraska. Turkey was introduced from Russia and is the oldest ancestral line. It was the foundation cultivar for hard red winter wheat in the

Table 1. The year of release, sources and pedigree history for 30 hard red winter wheat cultivars used for the study

Cultivar	Year	Source	Pedigree
Turkey	1874	Kansas	Selection from collections in U.S.A.
Kharkof	1905	Kansas	Selection from Kharkov, an introduction from Russia
Red Chief	1926	Kansas	Early Red Clawson/Red Arcadian
Cheyenne	1933	Nebraska	Selection from Crimean (C.I.1435)
Wichita	1944	Kansas	Early Blackhull/Tenmarq
Warrior	1960	Nebraska	Pawnee/Cheyenne
Sturdy	1966	Texas	Sinvalocho/Wichita//Hope/Cheyenne/3/2*Wichita/4/Seu Seun27
Scout 66	1967	Nebraska	Selection from Scout (CItr 13546)
Eagle	1970	Kansas	Selection from Scout
Baca	1973	Colorado	Selection from Scout
Sage	1973	Kansas	Agent/4*Scout
Buckskin	1973	Nebraska	Scout/4/Quivira//Tenmarq/3/Marquillo/Oro
Bennett	1978	Nebraska	Scout/3/Quivira/Tenmarq //Marquillo /Oro/4/Homestead
Centurk 78	1978	Nebraska	Selection from Centurk
Centura	1983	Nebraska	Warrior*5/Agent/NE68457/3/Centurk78
Colt	1983	Nebraska	Agate sib (NE69441)//391-56-D8/Kaw (TX65A1503-1)
Chisholm	1983	Oklahoma	Sturdy sib (TX391-56-D1-32)/Nicoma
Siouxland	1984	Nebraska	(Warrior*5/Agent)*2/Kavkaz
TAM 107	1984	Texas	TAM 105*4/Amigo
TAM 200	1986	Texas	TX7391-56-D8/Tascosa//Centurk*3/Amigo
Redland	1986	Nebraska	Selection from Brule (or Brule composite)
Arapahoe	1988	Nebraska	Brule/3/Parker*4/Agent//Beloterkovskaia 198/Lancer
Karl 92	1992	Kansas	Plainsman V/3/Kaw/Atlas 50//Park *5/Agent
Alliance	1993	Nebraska	Arkan/Colt//Chisholm Sib
Nekota	1994	Nebraska	Bennett/TAM 107
Niobrara	1994	Nebraska	TAM 105*4/Amigo//Brule
Pronghorn	1996	Nebraska	Centura/Dawn//Colt sib
Culver	1999	Nebraska	NE82419/Arapahoe
Millennium	2000	Nebraska	Arapahoe/Abilene/4/Colt/3/Warrior*5/Agent//Kavkaz
Wahoo	2000	Nebraska	Arapahoe*2/Abilene

Source: http://www.ars-grin.gov

Great Plains (Smith, 1995). "Cheyenne," a selection from "Crimean" (Clark, 1931), is believed to be the foundation of the Nebraska wheat improvement project and is an ancestor of many prominent cultivars. "Warrior" is a predominant parent of "Siouxland," "Centurk 78," and "Centura." "Scout 66," "Eagle," and "Baca" are direct selections from "Scout," the most prominent cultivar before the 1980s (Schmidt *et al.*, 1971). "Sage," "Bennett," and "Buckskin" are derived from "Scout." "Sturdy" was the first semidwarf hard red winter wheat available to growers (Atkins *et al.*, 1967) with considerable resistance to lodging, leaf rust (incited by *Puccinia tritica*) and stem rust (incited by *P. graminis* f. sp. *tritici*) races. Other semidwarf cultivars ("Colt," "TAM 107," and "TAM 200") were included in the study to examine the effect of introduction of semidwarf genes on agronomic and quality traits. "Redland" is a selection from "Brule" which is an important parent of both "Niobrara" and "Arapahoe" (Baenziger *et al.*, 1989). "Arapahoe" is the primary parent of widely grown cultivars like "Culver," "Millennium," and "Wahoo." "Alliance" (Baenziger *et al.*, 1995) was chosen as the most widely grown cultivar in Nebraska during this study (17% of the state wheat hectarage in 2002 and 12% in 2003).

Agronomic performance measurements

Field experiments were conducted under rain-fed conditions in Nebraska at Lincoln (fine montmorillonitic, mesic Typic Arguidoll), Mead (fine montmorillonitic,

Table 2. Monthly precipitation (in cm) for Lincoln, Mead, and North Platte, Nebraska, USA, for the winter wheat cropping seasons in 2001– 2002 and 2002–2003. Normally planting time is mid (North Platte) to late September (Lincoln and Mead) and normal harvest time in July. To conserve moisture, crops are not planted before wheat or harvested in July to allow moisture in July and August to be stored. Hence the monthly precipitation is given for 12 months rather than the 10-month growing season.

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	Total
Lincoln													
2001–2002	4.4	2.7	12.4	3.4	3.9	0.0	3.9	0.7	2.4	7.6	12.1	0.2	53.7
2002–2003	1.4	21.3	3.9	10.2	0.5	0.0	0.4	3.0	1.9	4.9	6.9	16.9	71.4
Mead													
2001–2002	2.0	5.6	5.5	5.3	5.5	0.4	2.1	1.0	2.2	7.1	7.5	1.3	45.5
2002–2003	3.6	18.7	2.9	8.3	0.4	0.0	0.8	2.2	1.6	6.3	12.5	8.9	66.1
North Platte													
2001–2002	5.2	15.1	6.5	1.2	2.4	0.4	0.4	0.3	0.3	1.5	2.6	3.2	39.0
2002–2003	1.7	2.4	2.5	3.6	0.0	0.0	0.0	0.4	2.2	9.0	4.6	8.2	34.6

mesic Typic Arguidoll), and North Platte (fine-silty, mixed, mesic Typic Argiustoll) during the 2002 and 2003 seasons. These testing sites represent Nebraska wheat growing areas with different environmental conditions (Peterson, 1992, Table 2 for monthly precipitation). An alpha lattice design with fifteen incomplete blocks of two plots each with three replications was used to evaluate cultivars under field conditions at all locations in each year. Plot size consisted of four rows each 2.4 m long with 30 cm between rows. The seeding rate was 54 kg ha^{-1}, and the planting time was from mid (North Platte) to late (Lincoln and Mead) September in 2001 and 2002. The seeding rate was chosen as being representative of traditional seeding rates for the diverse years the cultivars were grown and because recent research indicated that grain yield and end-use quality are unaffected by larger seeding rate changes than would be expected by differing cultivar kernel weights (Geleta *et al.*, 2002). Each plot was managed according to local recommendations for good growth and productivity. Ten plant characters were measured as described by Espitia-Rangel *et al.* (1999a) for each plot at all environments. The measurements include days to flowering, plant height, culm length, spike length, grain yield, grain volume weight, number of spikes per square meter, grain weight per spike, kernel number per spike, and kernel weight. Days to flowering were recorded as the number of days after 30 April when 50% of spikes in a plot had extruded anthers. At maturity, plant height was measured as the average height in cm from the ground to the tip of spike excluding awns. Prior to harvesting, ten random heads per plot were snapped to measure spike length and yield components. Spike length was determined as the average length from the node of last internode to the tip of ten heads excluding awns. Culm length was computed as the difference between plant height and spike length for each plot. All four rows of the plots were harvested for grain yield. Grain volume weight was measured on a 200 ml sample with a volumetric scale (Seedburo Equipment Co. Chicago, IL). The spikes were threshed and the kernels were counted to determine the mean grain weight per spike, the number of kernels per spike and kernel weight. The number of spikes per square meter was computed from plot grain yield, the number and weight of grains per spike.

End-use quality analyses

Grain micro-quality analyses were performed at the Lincoln Wheat Quality Laboratory, Department of Agronomy and Horticulture in the University of Nebraska using 50 g grain sample per plot from two replications. Quality analyses were made using grain from two replications to reduce the cost and previous research indicated little additional benefit by having a third replication. Each grain sample was tempered to a moisture content of 152 gH_2O kg^{-1} grain and milled in a Brabender Junior Laboratory mill (C. W. Brabender Instruments, Inc., South Hackensack, NJ). The flour was separated from the bran using a shaker (Strand, Minneapolis, MN) at 225 rpm for 90 s with a U.S. Standard Sieve No. 70 and weighed to estimate the flour yield per 50 g sample of grain. Flour protein content was determined by near-infrared reflectance (NIR) spectroscopy using flour samples from each plot following Method 39–70 (AACC, 1995). Flour mixing characteristics were evaluated on a 10 g flour sample using a Mixograph (National Manufacturing Co., Lincoln, NE) according to the Approved Method 54–40 (AACC, 1995)

with a constant water absorption of 610 $gH_2O\ kg^{-1}$ of flour. Mixograph mixing time (hereafter referred to as mixing time) was determined as the time in minutes required to reach peak dough resistance. Mixograph mixing tolerance (hereafter referred to as mixing tolerance) was rated based on the comparison against standard curves in the Nebraska Wheat Laboratory using a scale from low (0) to very high tolerance (7) with higher scores indicating greater tolerance of dough to overmixing using Approved Methods 54–40 (AACC, 1995; Baenziger *et al.*, 2001). Wheat lines with a mixing time of >3 min and a mixing tolerance scores of >3 are considered as having an acceptable end-use quality (Baenziger *et al.*, 2001). The SDS sedimentation volume, a predictive measure of protein quality (Graybosch *et al.*, 1995), was determined from a 2 g flour sample at a moisture basis of 140 $gH_2O\ kg^{-1}$ flour using the approved method 56–61 (AACC, 1995).

Statistical analyses of field and micro-quality trials

Analyses of variances (ANOVA) in each environment (location by year) were computed to identify the significant differences among cultivars for the individual traits. Error mean squares were tested for homogeneity of variances to ensure the appropriateness of combined analysis of variances. Agronomic data across six environments were analyzed for each trait by a PROC MIXED model considering the environments and cultivars as fixed effects whereas replications and incomplete blocks within environments as random effects. Microquality traits were analyzed using a PROC MIXED model for a randomized complete block design with two replications. Genetic gain over time was estimated by the regression coefficient from regressing cultivar means across six environments on the year of cultivar release for both agronomic and end-use quality characteristics. Phenotypic stability of cultivars for different traits was determined using the Eberhart & Russell (1966) regression methods. Stability regression coefficients, which measure cultivar response to varying environments, were estimated by regressing cultivar means on an environmental mean. The deviation sums of squares, which measure the consistency of responses across environments, were tested using *F*-tests. A cultivar with $b \leq 1$ and small deviation sums of squares was considered stable. The similarity of cultivars for grain yield stability was determined using hierarchical cluster analysis using average linkage method based on genotypic means, regression coefficients and squared deviation from regression for grain yield. All statistical analyses were performed using SAS software packages and procedures (SAS, 1996).

Results and discussion

Environment, cultivar and their interaction effects

The variances for individual traits in each environment were homogeneous; hence a combined ANOVA was conducted across six environments. The combined analysis of variance indicated highly significant differences among environments and cultivars for all agronomic traits (Table 3). The GEI was also highly significant for all agronomic traits except for grain weight per spike, kernel number per spike and kernel weight. Moreover, the significant GEI showed that cultivars had differential responses to various environmental conditions. The larger variances associated with environments than either genotypes or GEI, were previously reported in hard red winter wheat (Budak *et al.*, 1995; Espitia-Rangel *et al.*, 1999a; Geleta *et al.*, 2002; Campbell *et al.*, 2003). The mean squares of GEI were smaller (1.4–10 times) than the mean square of cultivars. When the interaction mean squares are considerably smaller than the cultivar mean squares in multi-environment tests, the cultivar rankings are expected to be relatively consistent (Gomez & Gomez, 1984). Consequently, regression analyses were used to examine the response and phenotypic stability of cultivars across environments for agronomic traits with significant GEI.

The ANOVA for end-use quality also showed significant differences among environments and cultivars (Table 2). The GEI was also highly significant for most end-use quality characteristics indicating that cultivars generally reacted differently for quality characteristics in different environments. Similar to previously reported results (Peterson *et al.*, 1992; Graybosch *et al.*, 1996; Espitia-Rangel *et al.*, 1999b; Budak *et al.*, 2003), the growing environment and the genotype were important determinants of wheat end-use quality. The GEI was smaller than environment and genotype for end-use quality characteristics, hence the cultivar ranks were expected to be consistent across environments. The significant GEI for both agronomic and end-use quality characters highlights the need for estimating genetic progress using genotypes from different eras by testing them together in multiple environmental conditions.

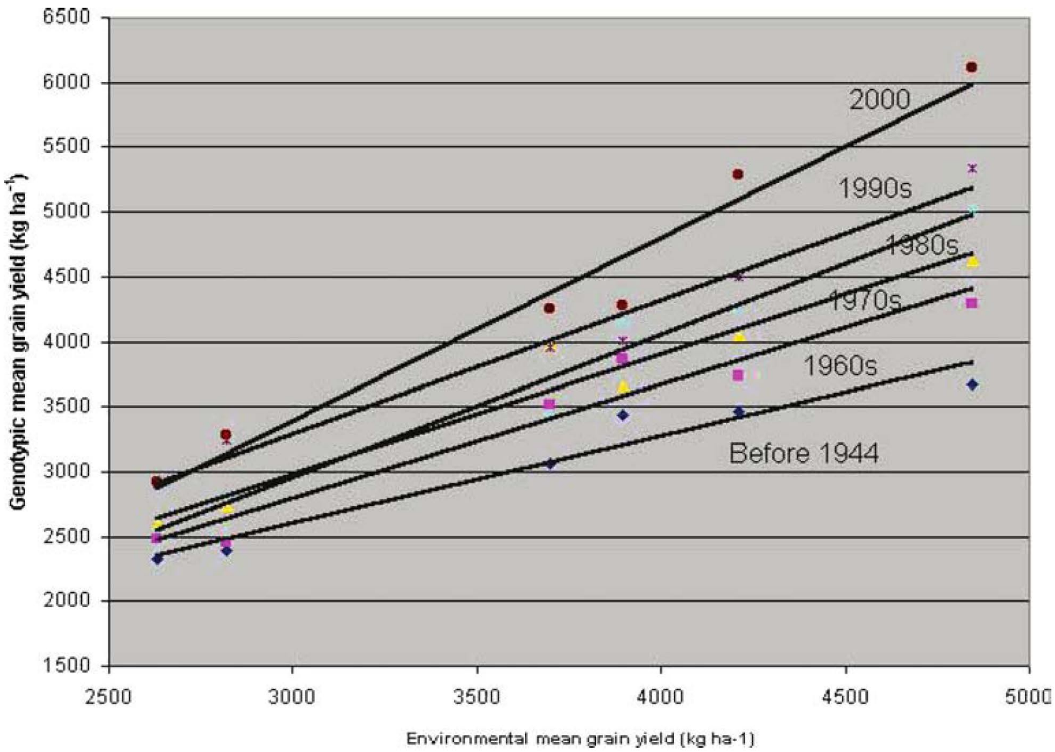

Figure 1. Grain yield responses of 30 hard red winter wheat cultivars tested at six Nebraska environments as an indication of genetic improvement over time by decade. The cultivars were grouped into six decades: before 1944 (Turkey, Kharkof, Cheyenne, Wichita), 1960s (Warrior, Sturdy, Scout 66), 1970s (Eagle, Baca, Sage, Buckskin, Bennett, Centurk 78), 1980s (Centura, Colt, Chisholm, Siouxland, TAM107, TAM200, Redland, Arapahoe), 1990s (Karl 92, Alliance, Nekota, Niobrara, Pronghorn) and 2000 (Millennium, Wahoo).

Phenotypic stability and response of cultivars

Grain yield responsiveness of cultivars to environments increased with more recent cultivar releases (Table 4). The average grain yield of modern cultivars released in 2000 was consistently higher and more responsive (less stable) than the average response of older cultivars even under lower yielding environments (Figure 1). The superiority of modern cultivars for grain yield was greatest in the high yielding environments. In agreement with previous research (Allen *et al.*, 1978; Rosielle & Hamblin, 1981; Kang, 1998), our results indicate that cultivars that are superior in high yielding environments could also produce at least equal or higher grain yield than older cultivars in lower yielding situations. It should be noted that lower yielding environments in this study have higher grain yields than many trials grown in more drought prone regions where tall wheat cultivars are preferred. Moreover, data from lower yielding environments are available during selection to insure that no line that performs poorly in lower yielding environments is released. Breeders select lines under favorable environments since these environments allow genotypes to express more of their maximum grain yield potential and often allow easier cultivar separation. Generally, older cultivars were low yielding, stable and less responsive to the favorable environments, whereas modern cultivars were high yielding and highly responsive to favorable environments. A few cultivars ("Pronghorn," "Sturdy," and "Buckskin") were the exceptions and had high grain yield at all environments and were stable (low *b* values; Figure 2).

Cluster analyses based on mean grain yield and its stability parameters (Figure 2) grouped stable ($b < 1.0$) and low yielding ancestral lines ("Turkey," "Kharkof," "Red Chief," "Cheyenne," and "Wichita") in one cluster. Other older cultivars released before 1970, except "Scout 66" and "Sage," were also stable for yield and hence clustered together. Cultivars released in the 1970s and thereafter were responsive to favorable environments and clustered together.

Plant height response of cultivars declined with the year of release (Table 3). Ancestral lines released before 1944 were the most responsive compared to cultivars released thereafter. Previous experiments on the

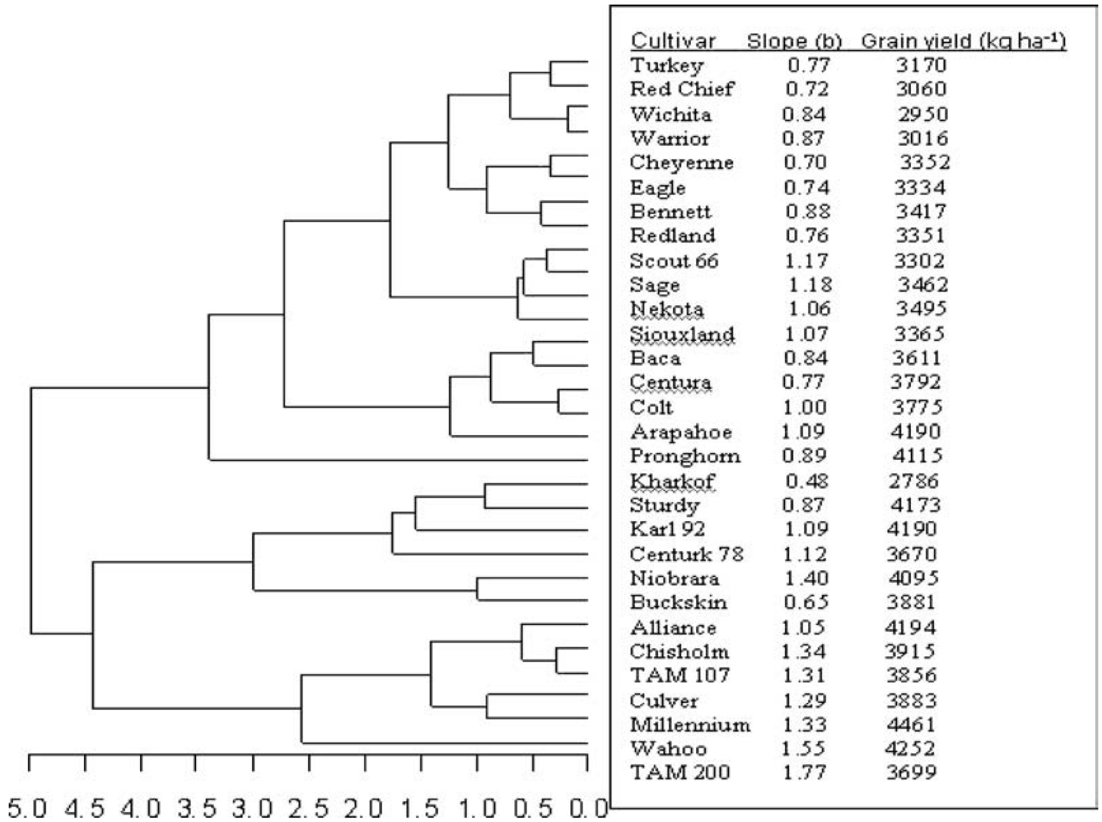

Figure 2. Dendrogram of 30 hard red winter wheat cultivars based on grain yield stability parameters and response to different Nebraska environments. Means, slopes and deviation from regression were used to cluster cultivars.

plant height response to different environments revealed that semidwarf cultivars were more stable for plant height compared to conventional height cultivars (Budak *et al.*, 1995). Similarly, cultivars released after the 1980s (generally semidwarf cultivars) were the most stable for plant height. In Nebraska, cultivars that are not too tall or too short are desirable for growing under its diverse environments to avoid lodging and mechanical combine harvesting problems (Budak *et al.*, 1995). Most modern cultivars are close to optimum plant height and hence perform well in both drought prone and high rainfall conditions of Nebraska. However, semidwarf cultivars tend to be better suited to the favorable environments, such as eastern Nebraska, since under drier conditions they may emerge poorly (resulting from a short coleoptile) and may be difficult to harvest due to their short plant height. Culm length was similar to plant height because spike length had small changes.

Cultivar response for days to flowering was linearly related to the year of release (Table 3). Ancestral lines released before 1944 and cultivars released in 2000 were less responsive for days to flowering, whereas cultivars released between these decades were highly responsive for flowering time. This result could be due to selection of medium maturity lines, that are mostly suitable for Nebraska environments and associated with high yield capacity. Breeders select lines for medium maturity since these lines avoid late season head frosting, and flower, fill grain, and mature before yield-limiting moisture and heat stress occurs.

Cultivars were responsive for the number of the spikes per square meters and newer cultivars had higher tillering capacity compared to older lines. As higher numbers of tillers bearing fertile spikes increases grain-yielding capacity of cultivars, breeders have selected lines with this trait. The response of cultivars was similar for grain volume weight and its relation with the year of cultivar release was non-significant since breeders selected for high grain volume weight to meet market standards.

Phenotypic stability analyses for end-use quality traits (Table 4) showed that the modern cultivars had higher flour yield and were more responsive than other cultivars for flour yield. Flour yield of these cultivars was high (over 60% extraction with a small experimen-

Table 3. Analysis of variance for ten agronomic traits and five end-use quality characteristics in 30 hard red winter wheat cultivars grown in Nebraska at Lincoln, Mead and North Platte during 2002 and 2003 crop seasons.

	Mean sums of squares																
Source of variation	d.f.	Days to flowering	Plant height (cm)	Spike length (cm)	Culm length (cm)	Grain yield (kg ha^{-1})	Kernel weight (g)	No. of kernels per spike	Spikes per m^2	Kernel weight (mg)	Grain volume weight (kg hL^{-1})	d.f.	Flour yield (g)	SDS-sedi-mentation value	Flour protein content	Mixing time (min)	Mixing tolerance (0–7)
Environments (E)	5	845.13**	17936**	11.19**	17887**	60349826**	0.99**	73387**	440116**	429**	467.08**	5	49.71**	167.10**	172.41**	13.07**	7.25**
Incomplete block or replication	264	2.49**	29.78**	0.199*	30.09**	148541**	0.02ns	15.82ns	4909 ns	9.79ns	1.29**	6	15.75**	15.49**	1.91**	1.11**	5.60**
Cultivars (C)	29	34.07**	513.90**	1.17**	499.37**	1043403**	0.049**	39.19**	12955**	20.13*	8.77**	29	12.67**	116.65**	3.88**	6.28**	4.79**
C × E	145	3.796**	50.53**	0.22**	51.35**	400467**	0.02ns	14.94ns	6627**	14.55ns	1.99**	144	0.93**	9.17**	0.46*	0.35ns	0.66**
Error	96	1.36	18.68	0.14	18.25	117451	0.02	14.15	3682	12.08	0.59	172	0.59	3.32	0.34	0.27	0.26
Mean		28	97	7.47	89	3650	0.92	29	404	31.78	82.17		33.58	30.69	11.06	3.70	3.46
C.V. (%)		5.22	5.36	5.73	5.82	10.26	14.15	13.51	16.72	10.15	1.69		3.12	6.29	5.66	14.8	19.31

Note. ANOVA was performed using incomplete block and replication within environments for agronomic traits and end-use quality characteristics, respectively.
*, ** Significant and highly significant at 5% and 1% probability level, respectively; d.f. = degrees of freedom

Table 4. Phenotypic stability parameters and genetic gain for agronomic traits in 30 hard red winter wheat cultivars by decades

Character		Before1944	1960s	1970s	1980s	1990s	2000	b^{++}	$S.E._b$
Days to flowering (day)	$\bar{x}$	30.12	29.54	28.52	27.77	27.89	28.92	–0.032*	0.014
	b^+	0.77	1.12	1.23	1.08	0.86	0.96		
	S_d^2	2.46	2.71	3.48	3.53	3.63	2.75		
Plant height (cm)	$\bar{x}$	110	103	100	90	94	96	–0.208**	0.05
	b^+	1.18	1.21	1.04	0.89	1.01	0.95		
	S_d^2	43.53	43.13	52.54	22.19	30.84	31.42		
Spike length (cm)	$\bar{x}$	7.71	7.77	7.31	7.40	7.39	7.47	–0.004	0.002
	b^+	1.37	1.14	0.92	1.11	0.85	0.69		
	S_d^2	0.37	0.29	0.21	0.16	0.14	0.18		
Culm length (cm)	$\bar{x}$	102	95	93	83	86	88	–0.203	0.045
	b^+	1.18	1.20	1.04	0.89	1.01	0.95		
	S_d^2		43.22	45.12	52.83	22.99	29.56	30.03	
Grain yield (kg ha^{-1})	$\bar{x}$	3063	3389	3608	3628	3956	4133	10.44**	2.00
	b^+	0.70	0.90	0.93	1.19	1.03	1.22		
	S_d^2	125934	254266	310447	238768	344066	215258		
No. of spikes/m^2	$\bar{x}$	377	382	411	378	428	420	0.386	0.242
	b^+	1.02	0.95	0.69	1.21	1.02	1.17		
	S_d^2	4094	3497	6705	4275	6345	6087		
Grain volume weight (kg hL^{-1})	$\bar{x}$	83.43	82.41	82.68	81.08	81.07	81.47	–0.015	0.01
	b^+	1.10	0.92	0.98	1.14	0.94	0.90		
	S_d^2	1.22	1.16	1.70	1.68	1.86	1.88		
Grain weight/spike (g)	$\bar{x}$	0.86	0.90	0.90	0.97	0.94	1.00	0.002**	0.0004
No. kernels/spike	$\bar{x}$	26	29	29	31	30	32	0.015**	0.016
Kernel weight (mg)	$\bar{x}$	32.22	31.14	31.69	31.54	32.29	31.90	0.0014	0.011

Note. $\bar{x}$ is mean of each trait across six environments; S_d^2 is sums of squares of deviation from regression; b^+ is regression coefficients computed by regressing trait mean by decades on the environmental means and all regression coefficients were significantly different from zero at 1% level; b^{++} is regression coefficients used as measure of genetic gain and computed by regressing the genotypic means on the year of cultivar release.
*, ** = significant and highly significant from zero at the 5% and 1% probability level, respectively.

tal mill) since lines were tested and selected for high flour yield before release. The greater responsiveness of modern cultivars for flour yield showed that they produce more flour yield under environments conducive for plump grain development.

Flour protein content of older lines was higher than newer cultivars since ancestral lines had lower grain yields. Breeders select cultivars with high grain yield and reasonable protein content. There was no general pattern for flour protein content stability by decade, though the oldest cultivars were the most stable. Modern cultivars were more responsive for SDS-value and mixing tolerances and less stable for these traits relative to lines released before the 1960s. This result was expected and desirable since lines with higher mixing tolerance (>3) are currently preferred and selected for (Baenziger *et al.*, 2001). The older cultivars were stable and had shorter mixing tolerances (Table 5), which were preferred in the baking processes when they were released.

Variability and trends of genetic improvement

Significant regression coefficients were observed for all agronomic traits regressed on the year of cultivar release except for the spike length, number of spikes per square meter and kernel weight (Table 4). Compared to ancestral cultivars, breeders have selected cultivars that are earlier, shorter in plant height, culm length and lower in grain volume weight. This result was in agreement with previously reported results (Feyerherm *et al.*, 1984; Cox *et al.*, 1988; Donmez *et al.*, 2001). Selection by breeders for higher grain yield and yield components has resulted in steady improvement in these traits (Cox *et al.*, 1988; Donmez *et al.*, 2001: Khalil

Table 5. Phenotypic stability parameters and genetic gain for end-use quality traits in 30 hard red winter wheat cultivars by decades

Decade	Flour yield (g) $\bar{x}$	Flour yield (g) b^{1+}	Flour yield (g) S_d^2	Flour protein content (%) $\bar{x}$	Flour protein content (%) b^+	Flour protein content (%) S_d^2	SDS-sedimentation value (m^3) $\bar{x}$	SDS-sedimentation value (m^3) b^+	SDS-sedimentation value (m^3) S_d^2	Mixing time (min) $\bar{x}$	Mixing tolerance (%) $\bar{x}$	Mixing tolerance (%) b^+	Mixing tolerance (%) S_d^2
Before 1944	32.98	1.01	1.68	11.85	0.94	0.52	28.14	0.70	5.79	3.00	2.93	–0.16	0.48
1960s	34.18	0.45	0.94	11.06	1.04	0.33	28.72	1.47	6.29	2.90	3.18	0.24	0.24
1970s	33.92	0.87	0.92	11.21	1.02	0.43	32.97	0.71	4.59	3.84	3.92	1.03	0.57
1980s	33.31	1.11	1.05	10.88	0.98	0.44	31.43	1.03	6.78	3.96	3.43	1.57	0.64
1990s	33.56	1.20	0.47	10.74	1.00	0.37	31.23	1.08	4.86	4.14	3.67	1.67	0.33
2000	34.30	1.15	0.73	10.64	1.05	0.57	28.31	1.61	6.61	4.03	3.25	0.76	0.52
b^{++}	0.007			–0.014**			0.035			0.013*	0.006		
$S.E._b$	0.01			0.003			0.02			0.004	0.004		

Note. $\bar{x}$ = mean of each trait across six environments; S_d^2 = sums of squares of deviation from regression; b^+ is regression coefficients computed as by regressing trait mean by decades over the environmental means and all regression coefficients were significantly different from zero at 1% level; b^{++} is regression coefficients used as measure of genetic gain and computed by regressing the genotypic means over the year of cultivar release.
*, ** = significant and highly significant from zero at the 5% and 1% probability level, respectively.

et al., 2002a). Differences in grain yield among cultivars were highly significant and increased over time ranging from 2786 to 4461 kg ha^{-1} (Figure 2). The genetic gains for grain yield (10.4 kg ha^{-1} yr^{-1}) observed among the cultivars in this study was similar to those reported by Cox *et al.* (1988) who found increased grain yield (16.2 kg ha^{-1} yr^{-1}) in 38 hard red winter wheat cultivars released between 1919 and 1980 in Kansas. Khalil *et al.* (2002a) reported a grain yield increase of 11.3 kg ha^{-1} and 18.8 kg ha^{-1} based on 12 hard red winter wheat cultivars tested under dual purpose and grain-only growing conditions, respectively, in Oklahoma. For the breeding period of 1873 to 1995, Donmez *et al.* (2001) reported mean genetic gain of 0.44% yr^{-1} based on 14 hard red genotypes grown under protected conditions from lodging and leaf rust in Kansas.

Grain yield is a complex plant trait and a function of its several other traits. The genetic gain for grain yield was related to a significant increase in kernel weight (r = 0.62**) and kernel number per spike (r = 0.52**). Breeders selected for earlier and shorter (e.g. semidwarf) lines. Average flowering date ranged from 23 to 32 days with an average of 28 d after 30 April (Table 4). Ancestral lines had the longest time to flower (32 days) whereas most short and semidwarf lines developed in the Southern States of the Great Plains had shorter flowering times. Flowering date is an important trait (Baenziger *et al.*, 2001) for the prediction of the cultivar performance under different Nebraska environments.

Plant height decreased with the year of release (0.21 cm yr^{-1}) (Table 4). Ancestral lines released before 1944 were tall (average height >100 cm) whereas most cultivars released afterwards were semidwarf. The exception was "Pronghorn" (104 cm), a modern tall cultivar deliberately developed for drought prone conditions (Baenziger *et al.*, 1997). Reduction of wheat plant height, mainly achieved with the introduction of reduced height (*Rht*) genes (Borell *et al.*, 1991), accounted for dramatic grain yield increases in the 1970s and 1980s. Semidwarf cultivars have better harvest index and are more resistant to lodging (Smith, 1995), but can be difficult to harvest under low moisture conditions. Similar decreasing trends were observed among cultivars for culm length and this was related to selection for shorter plant height.

Grain weight per spike increased with the year of release (0.86–1.00 g) and its genetic gain was highly significant (Table 4). Cultivars were also substantially different for the number of kernels per spike, which ranged from 26 to 32. These results reveal that modern cultivars had higher kernel weight and kernel number per spike than ancestral and older cultivars, and equal or better grain volume weight. Modern cultivars have more favorable genes controlling spike morphology, spike productivity (number of grains per spike and their weight) and floret fertility contributing to their higher yielding capacity.

Non-significant genetic gain was observed for grain volume weight since all cultivars must meet a minimum standard. Based on the 12 hard red winter wheat cultivars evaluated in Oklahoma, Khalil *et al.* (2002a) observed no linear trend of grain volume weight with the year of release.

Cultivars are selected for high flour yield (31–35 g flour from 50 g of grain); however, the variability among cultivars for flour yield was low and no trend was found. Over time, plant breeders have indirectly se-

lected for cultivars with lower flour protein content by selecting for higher grain yield, however they have also selected for higher SDS-sedimentation value (Table 5). In agreement with Kibite & Evans (1984), the decreasing trend of flour protein content (0.014 g year^{-1}) most likely related to increased grain yield. The reduced protein content disagreed with Cox *et al.* (1989) and Khalil *et al.* (2002b) who obtained positive and no correlations of protein content with grain yield, respectively. The reduction of flour protein content was offset by an increase in mixing time and tolerance and to a lesser extent by high SDS sedimentation volumes, an indicator of gluten strength. Cultivars were bred for higher mixing time and tolerance (Baenziger *et al.*, 2001) with adequate protein content, preferably 120 g of protein per kg grain. Genetic gain for mixing time (0.01 min yr^{-1}) and mixing tolerance (0.006 units yr^{-1}) was also reported (Khalil *et al.*, 2002b). In Kansas, Cox *et al.* (1989) also found positive genetic gain (0.06 min yr^{-1}) for mixing time. According to Baenziger *et al.* (2001), lines with >3 min for mixing time and >3 for mixing tolerance, preferably >4 for both, are preferred for baking quality. Considering the genetic improvement in mixing time and mixing tolerance, only a few cultivars would be unacceptable for mixing time (4 genotypes) and mixing tolerance (5 genotypes), hence these winter wheat cultivars were successfully selected for high mixing properties. "Wichita" had the lowest mixing time (2.57 min) and mixing tolerances (1.91 min.) while newer cultivars "Pronghorn" and "Karl 92" had the highest mixing time (4.94 min.) and mixing tolerance (4.93), respectively (Table 5). Relative to older cultivars, despite lower protein content, the modern cultivars had average mixing time and high tolerance to over mixing, making them desirable for the milling and baking industries (Baenziger *et al.*, 2001).

Conclusions

Selection in wheat for grain yield and end-use quality has resulted in steady improvements in these traits over the past 125 years in Nebraska. Highly significant differences among environments and cultivars were observed for all agronomic and end-use quality traits showing the diversity of environments and cultivars. Genotype X environment interaction was significant for all characters except for grain weight per spike, kernel number per spike, kernel weight, and mixing time. The higher grain yields of modern cultivars in all environments indicate that modern cultivars were selected for improved tolerance to environmental stresses in both low yielding environments and favorable environments. Phenotypic stability analyses revealed that more recently developed cultivars were highly responsive for grain yield and yield components whereas the old cultivars were more stable. Older cultivars were highly responsive for plant height and culm length. Genetic gain for grain yield was accompanied by increased kernels per spike, grain weight per spike and spikes per square meter, as well as, shorter plant height and appropriate maturity. Breeders have reduced flour protein content, but improved the end use functional quality.

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