Historical shifts in the seed mineral micronutrient concentration of US hard red winter wheat germplasm†‡

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Abstract: The yield of wheat (*Triticum aestivum* L. em. Thell) has greatly improved through breeding, but it is not known how this has affected seed micronutrient content. In the present study, the iron (Fe), zinc (Zn), copper (Cu), and selenium (Se) content of seed of 14 US hard red winter wheat varieties from production eras spanning more than a century was measured. The seed that was analyzed was obtained from a replicated field trial conducted at two locations in Kansas. The Fe, Zn, and Cu content was obtained by inductively coupled plasma emission spectroscopy (ICPES) and Se content was obtained by hydride-generated atomic absorption spectrometry (HG-AAS). Significant effects of location on micronutrient content of seed were observed. Similarly, depending on the micronutrient, significant differences in seed micronutrient content between varieties were detected at one or both locations. A significant negative regression of seed Zn content on both yield and variety release date was observed at both locations, while seed Fe content exhibited a significant negative regression on yield and variety release date at one location. Regression of seed Se content on variety release date was significant and negative at one location. These results suggest that genetic gains in the yield of US hard red winter wheat have tended to reduce seed Fe, Zn, and Se concentrations. However, the extent to which this effect manifests itself is influenced by environmental effects.
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INTRODUCTION

Wheat is one of the founder crops associated with modern human civilization. Grain of wild relatives of wheat was collected as a food by humans dating back more than 10 000 years, and the cultivation and domestication of wheat and its relatives also extend far back into prehistory.[1] Today, wheat is the most widely grown food crop and global production of wheat is higher than for any other such crop, with nearly 600 million metric tons produced annually.[2] Wheat provides more nutritional sustenance to humans than any other crop and thus arguably remains the most important staple crop for humans.

While wheat is recognized primarily as a source of energy and protein in human diets, it also contributes many other important nutrients. Wheat contributes a significant amount of the vitamins niacin, thiamin, vitamin E and B_6 to the human diet, and contains several others such as riboflavin in lesser abundance.[3] Further, wheat is a source of many mineral nutrients. This includes mineral macronutrients such as phosphorus (P), potassium (K), magnesium (Mg), and calcium (Ca), as well as mineral micronutrients including iron (Fe), zinc (Zn), copper (Cu), and manganese (Mn).[4] These minerals are essential for both humans and plants. Further, wheat serves as an important source of selenium (Se) in human diets,[5] even though this mineral has not been shown to be essential in plants, as it is in animals.

Wheat yields have increased dramatically over time. In the early 1900s, the average wheat yield was estimated to be approximately 860 kg ha^{-1}.[6] Today, the average yield of wheat is estimated to be more than three times this amount.[2] Particularly significant yield gains have been made during the last 50 years, where the doubling of global wheat production that has occurred in this period can be attributed solely to increased yield and not to increased land under cultivation.[7] While there are several factors that underlie this yield increase, one of the most prominent

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is the contribution of genetic improvement through breeding.[8]

The global incidence of mineral micronutrient deficiencies in humans is in many instances high. For example, iron deficiency is the most common dietary deficiency that affects billions of individuals.[9] Further, Se deficiency is prevalent in many areas of the world, especially portions of East Asia, and many areas of Europe have Se intakes below the US recommended daily allowances.[10] Both Zn and Cu deficiency may also be prevalent in some human groups.[11,12] In part, these micronutrient deficiencies can be attributed to the lack of diversified diets and a reliance upon staple crops, which do not supply adequate minimum daily requirements of these minerals. This has led to the suggestion that development of staple food varieties that have enhanced levels of these mineral micronutrients (biofortification) would ameliorate the incidence of these mineral micronutrient deficiencies in humans.[13] An additional benefit may be gained from biofortification for Se, since supplemental Se intake at levels exceeding minimum recommended daily allowances has been associated with a reduced incidence of some forms of cancer in humans.[14] Thus, increasing the levels of Se may have health benefits for humans that extend beyond simply meeting the basic nutritional requirement for Se. The preeminent role of wheat in human diets makes it a logical candidate for biofortification efforts.

While biofortification of staple foods to address nutrient deficiencies is an enticing concept, there is much to understand about the potential impact that such efforts might have on other important traits. For instance, it is not clear whether selection for increased mineral micronutrient content might negatively affect yield or other important agronomic and end use characters. This could occur if genes that increase mineral content are linked with genes that have a deleterious effect on other desired traits, or it could occur as a consequence of trait associations.

If a negative association between seed mineral concentrations and yield exists in wheat, this should be reflected in progressive shifts in mineral concentrations in wheat varieties representing a historical continuum of genetic improvement for yield that has occurred during the modern era of plant breeding. In the USA, hard red winter wheat (HRWW) has been grown on the Great Plains since the latter part of the 19th century,[15] and today HRWW is the largest class of wheat produced in the USA.[2] The well-documented history of HRWW improvement and the large gains in yield that have occurred in the last several decades due to genetic improvement by breeding provide an ideal opportunity to determine whether mineral micronutrient content is negatively associated with selection for improved productivity. The goal of this study was to determine whether seed mineral micronutrient concentrations in HRWW have been altered as genetic gains in yield have increased.

MATERIALS AND METHODS

Plant materials

The HRWW seed used for this study was kindly provided by Dr Allan Fritz (Kansas State University). The seed had been harvested as part of a previous field study to examine changes in agronomic characters among a selected set of 'landmark' US HRWW genotypes.[16] Detailed information on this previous study, including growth conditions, experimental design, and other details, can be found in an earlier publication.[16] Briefly, the experimental design of the earlier study involved growing 14 different wheat genotypes representing different production eras ranging from 1873 (the year of introduction of HRWW to the Great Plains) through the modern breeding era starting in the early 1940s until the late 1990s (Table 1), in replicated trials at two different locations in Kansas (Hutchinson and Manhattan) in the 1998–99 season. The genotypes were grown in a split plot design, with the main plots being varieties and the subplots being either a netted and sprayed section of the plot to protect against fungal disease and lodging, or unprotected sections. There were four replications per genotype at each location. Seed supplied by Dr Fritz for use in this study had been harvested from the four replicates for each genotype for the netted and sprayed subplots, so as to not have disease or lodging confound our results.

Mineral analysis

For this study, the seed concentrations of Fe, Zn, and Cu were obtained by inductively coupled plasma emission spectroscopy (ICPES). Briefly, seed samples were dried at 60 °C overnight and weighed subsamples of individual seed samples (0.5 g) were wet-digested in a mixture of nitric acid and perchloric acid and analyzed for mineral element content using ICPES, with appropriate standards and reference materials as described previously.[17] Seed Se concentrations were

Table 1. Hard red winter wheat genotypes assayed for seed mineral element concentrations. Information on released varieties is from the US National Genetics Resources Program (http://www.ars-grin.gov)

Genotype	Year of release	Location of development
Turkey	1873	Introduced
Pawnee	1942	Nebraska
Wichita	1944	Kansas
Triumph 64	1964	Oklahoma
Scout 66	1967	Nebraska
Eagle	1970	Kansas
Newton	1978	Kansas
Arkan	1982	Kansas
TAM 107	1984	Texas
Karl 92	1992	Kansas
Jagger	1993	Kansas
Ike	1994	Kansas
2137	1995	Kansas
KS941064-6	(2000)[a]	Kansas

[a] Advanced breeding line.

determined by hydride-generated atomic absorption spectrometry (HG-AAS), as described previously.[18] Samples were ground, and weighed quantities (0.5 g) of each sample were digested in nitric acid followed by ashing in a muffle oven at 490 °C for 14 h and resuspension in hydrochloric acid prior to analysis. Analytical runs included three blanks and wheat flour standards (NBS 1567a Wheat Flour, National Bureau of Standards, Gaithersburg, MD, USA). Samples were analyzed using a Perkin Elmer 5100PC AAS FIAS with a hydride generator (Perkin Elmer, Wellesley, MA, USA).

Data analysis

In the original study from which the analyzed seed was harvested,[16] the experiment was designed as a split plot with varieties representing main plots. We were only interested in examining the seed from the sprayed and treated subplots to avoid the lodging and disease differences that exist between genotypes from confounding our analysis. Thus in this study the experimental data was treated as a randomized complete block design. Two-factor analysis of variance was employed to identify varietal differences among genotypes for each of the micronutrients of interest; each of the locations was analyzed separately. Subsequently, pairwise comparisons of differences between variety means were completed with the Tukey HSD test statistic. Pearson correlation analysis was used to examine both for associations between mineral concentrations in wheat seeds between locations, and to examine the association between the concentrations of different minerals at each location. The relationship between yield and seed mineral concentrations was investigated by linear regression analysis. Similarly, regression analysis was used to examine for a dependence of seed mineral micronutrient concentrations on variety age.

RESULTS

Genotypic differences in seed mineral micronutrient content

Descriptive information on seed mineral concentrations at each location is provided in Table 2. The relative concentration of the minerals at both locations was Fe > Zn > Cu > Se. For the first three of these minerals, concentrations were all above 1 $\mu g\,g^{-1}$, although Cu was present at concentrations one order of magnitude lower than Fe and Zn (Table 2). The means and relative ranges of seed Fe, Zn and Cu concentrations tended to be higher at Manhattan than at Hutchinson, and was most evident for Cu concentration, which was twice as high at Manhattan. Paired two-sample *t*-tests confirmed that the seed Fe, Zn, and Cu concentrations in the wheat at Manhattan *versus* Hutchinson were significantly different, with mean concentrations for all three minerals being higher in the wheat grown at Manhattan. The opposite result was observed for Se, for which the mean seed concentration in the wheat grown at Hutchinson was nearly eight times greater than that in the wheat grown at Manhattan (0.36 $\mu g\,g^{-1}$ *versus* 0.046 $\mu g\,g^{-1}$) (Table 2).

Analysis of variance identified significant differences between genotypes in seed Fe, Zn, Cu and Se concentrations at both locations, with the exception of Se at Manhattan. At Hutchinson, where seed Fe, Zn, and Cu concentrations were lower than in the wheat grown at Manhattan, highly significant differences among genotypes ($P < 0.001$) were detected for all four of the micronutrients (Table 3). In contrast, at Manhattan the genotypic differences for Fe and Zn were detected at a *P*-value of just 0.05, while the varietal differences for seed copper concentration were highly significant ($P < 0.001$) (Table 3).

Pairwise comparisons of varietal means suggested that at Manhattan, the seed micronutrient concentrations of the oldest variety analyzed, Turkey, were not significantly higher than those of any other genotype (Table 3). A different pattern emerged at Hutchinson, where Turkey exhibited the highest seed concentrations of Fe, Zn, and Se (Table 3). Here, pairwise comparisons indicated that the seed Fe concentration of Turkey was significantly higher than that found in all of the other varieties. Similarly, at this location the seed Zn and Se concentrations of Turkey were significantly higher than nine and five of the more modern varieties, respectively, with a clear trend for lower seed Zn and Se in progressively newer varieties (Table 3).

Relative ranking of varieties for seed mineral concentrations

Despite the fact that significant differences in absolute levels of the minerals were detected between the wheat grown at Manhattan and Hutchinson, an examination of seed micronutrient data from both locations revealed a number of cases where the same genotype exhibited either the lowest or highest concentration of a particular micronutrient at both locations. For instance, TAM 107 had the lowest Fe and Jagger had the lowest Zn concentration at each location, and Triumph and Turkey had the highest Cu and Se concentrations at each location, respectively (Table 3). Correlation analysis was undertaken to further examine genotype–environment interactions for mineral micronutrient differences between genotypes. For all

Table 2. Summary of means and ranges of seed mineral micronutrient concentrations in 14 different hard red winter wheat varieties grown at Hutchinson, KS, and Manhattan, KS, in the 1998–99 growing season. Values expressed as $\mu g\,g^{-1}$

	Hutchinson		Manhattan	
Element	Mean	Range	Mean	Range
Fe	31.4	24.4–42.8	33.7	30.2–38.3
Zn	20.9	16.0–26.3	29.3	26.1–33.9
Cu	2.12	1.74–2.82	4.2	3.68–5.68
Se	0.36	0.28–0.48	0.045	0.039–0.055

Table 3. Mean seed micronutrient concentrations in 14 hard red winter wheats grown at two locations in Kansas in 1998–99. Varieties are listed in order of their date of release

	Manhattan				Hutchinson			
Variety	Fe[a]	Zn	Cu	Se	Fe	Zn	Cu	Se
Turkey	37.2	29.9	3.90	55.3	42.8	26.3	2.54	478
Pawnee	32.9	32.8	4.23	48.0	32.8[b]	25.5	2.03	349
Wichita	33.1	30.9	4.89	50.4	28.0[b]	21.8	2.34	362
Triumph	36.8	33.9	5.68	39.0	32.5[b]	22.6	2.82	357
Scout 66	32.6	29.4	4.06	47.9	34.8[b]	23.0	1.82	401
Eagle	30.9	28.6	4.19	48.1	30.2[b]	20.9[b]	1.95	367
Newton	34.4	27.1	3.83	44.1	35.4[b]	18.7[b]	1.74[b]	383
Arkan	36.0	29.1	3.68	40.0	32.9[b]	20.7[b]	1.77	278[b]
TAM 107	30.2	26.6	4.02	46.5	24.4[b]	17.5[b]	1.91	316[b]
Karl 92	35.0	30.0	4.21	47.2	30.5[b]	20.7[b]	1.94	321[b]
Jagger	30.6	26.1	3.68	44.2	26.7[b]	16.0[b]	2.13	329
Ike	38.3	29.8	3.87	45.9	34.4[b]	20.8[b]	1.97	315[b]
2137	33.3	29.4	4.71	43.5	27.9[b]	20.7[b]	2.48	478
KS941046-6	30.9	26.6	3.87	41.5	26.7[b]	18.2[b]	2.19	299[b]
AOV *F*-value	2.47*	2.19*	1.22***	NS	15.10***	8.27***	3.97***	3.80***
HSD (5%)	8.3	7.6	1.18		6.1	4.9	0.80	152

[a] Values expressed as $\mu g\,g^{-1}$, except Se, expressed as $ng\,g^{-1}$.
[b] Means that differ significantly from that of Turkey.
* $p < 0.05$
** $p < 0.001$
*** $p < 0.001$

the minerals except Se, there was a highly significant and positive correlation between the levels of a given mineral in the genotypes at one location and the levels measured at the other location (Table 4). This result is illustrated by comparing plots of seed micronutrient concentrations of the different varieties at both locations (Fig. 1). The congruence between relative mineral micronutrient contents in many genotypes at both locations is particularly evident for Fe and Zn, and to a lesser extent for Cu (Fig. 1).

Phenotypic correlations between seed micronutrient concentrations

At Hutchinson, only one of the six possible pairwise combinations of micronutrients (Fe/Zn) exhibited a significant correlation ($P < 0.01$), which was positive (Table 4). The Fe/Zn correlation was also significant ($P < 0.05$) and positive at Manhattan, as was Cu/Zn ($P < 0.01$) (Table 4). Correlations between the mineral micronutrients and additional selected elements for which seed concentrations were obtained from ICPES were also analyzed. In particular, phosphorus (P) and sulfur (S) concentrations were examined for possible correlations with the micronutrients. The Zn/P correlation was highly significant and positive at both locations, but P concentration was correlated with another micronutrient in just one other comparison (P/Cu at Manhattan). Interestingly, the results of the correlation analysis between S concentration and the micronutrient concentrations were dramatically different between the two locations. At Hutchinson, S concentration was significantly and positively correlated with each of the micronutrients except Cu. In contrast, at Manhattan, no significant correlations were detected between S and the micronutrients (Table 4).

Table 4. Correlation coefficients between seed mineral micronutrient concentrations in wheat grown at two different locations in Kansas in 1998–99. Results for the Hutchinson KS location are shown above the diagonal, and the Manhattan KS results are below the diagonal. Interlocation correlation coefficients for mineral concentrations are located on the diagonal, in bold

	Fe	Zn	Cu	Se	P	S
Fe	**0.72****	0.71**	0.07	0.45	0.50	0.71**
Zn	0.55*	**0.78*****	0.33	0.49	0.87***	0.88***
Cu	0.18	0.71**	**0.72****	0.46	0.16	0.26
Se	0.01	0.08	−0.18	**0.48**	0.34	0.53*
P	0.42	0.91***	0.76**	0.02	**0.72****	0.86***
S	−0.31	0.25	0.40	0.25	0.41	**0.33**

* $p < 0.05$
** $p < 0.001$
*** $p < 0.001$

Relationship between seed micronutrient concentration and yield improvement

To examine how several decades of genetic gains in yield have influenced seed micronutrient concentrations in US HRWW, seed mineral micronutrient concentrations were regressed on yield, using yield data reported from the experimental plots that provided seeds for the present study.[16] In three cases, this regression was significant. This included seed Zn content at both Hutchinson and Manhattan ($r^2 = 0.73$, $P < 0.0001$; and $r^2 = 0.39$, $P < 0.05$, respectively), and seed Fe content at Hutchinson ($r^2 = 0.33$, $P < 0.05$) (Fig. 2). The regression coefficient is a direct measure of the mean change in

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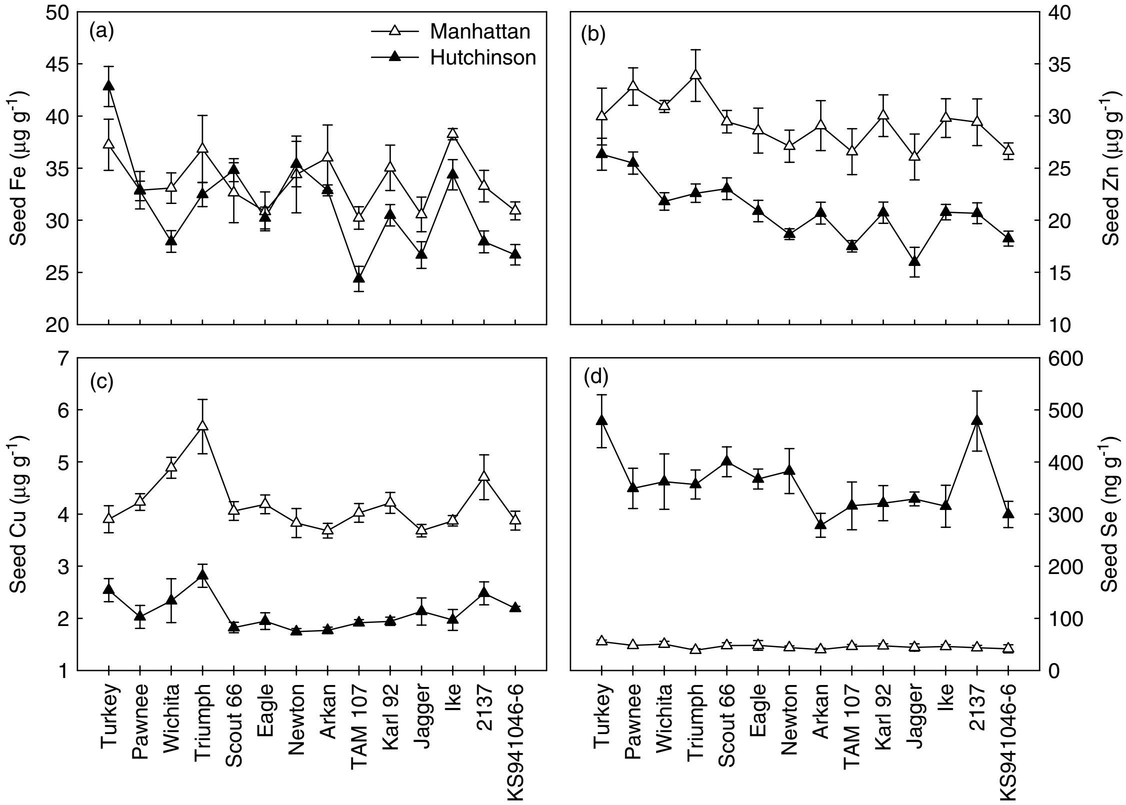

Figure 1. Seed micronutrient concentrations of HRWW varieties plotted by date of variety release. The oldest variety (Turkey) is at the left and the newest genotype (KS941946) is at the right. Filled triangles are mean seed micronutrient concentrations obtained at Hutchinson, KS; open triangles are mean seed micronutrient concentrations obtained at Manhattan, KS. Bars represent standard errors. (a) Fe; (b) Zn; (c) Cu; (d) Se.

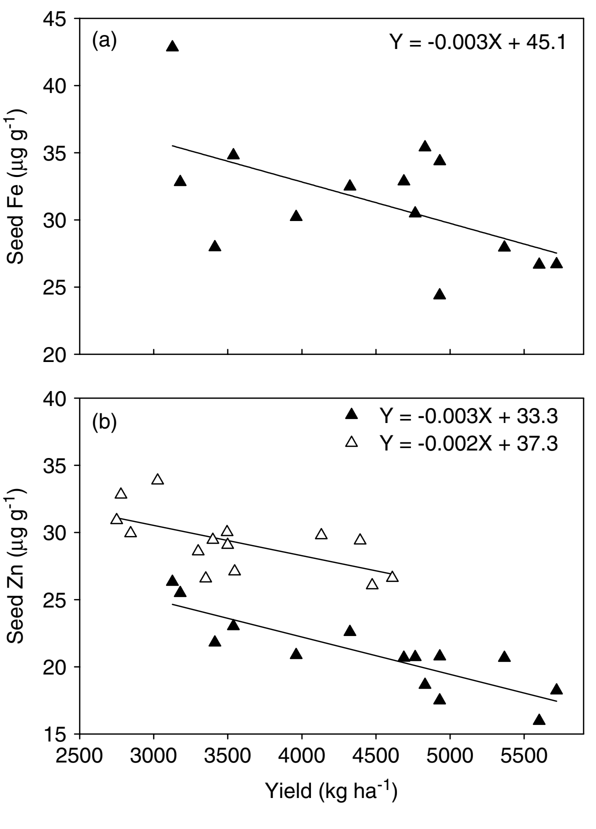

Figure 2. Significant regressions of wheat seed mineral micronutrient contents on yield. Yield data used for regression analysis were presented in an earlier study.[16] Filled and open triangles are data points for Hutchinson and Manhattan, KS, respectively. The best-fit simple linear regression line is shown.

seed micronutrient content due to yield. At Hutchinson, an average loss of approximately 3.0 ng kg^{-1} yield increase for both seed Fe and Zn content was observed. At Manhattan, an average seed Zn loss of 2.3 ng kg^{-1} yield increase was observed (Fig. 2).

Similarly, the linear relationship between seed micronutrient content and date of variety release revealed trends similar to those observed for regression of micronutrient contents on yield (Fig. 3). For this analysis, a release date of 1919 was used for Turkey, since by this date it was the dominant HRWW wheat grown in the Great Plains and modern hybridization-based breeding in this region were starting to be initiated.[15] At the Hutchinson location, regression of seed Fe and Zn contents on date of variety release were each significant ($P < 0.05$ and $P < 0.0005$, respectively). For seed Fe content, the r^2 value was 0.36 and the mean decrease in seed Fe was 0.12 µg g^{-1} y^{-1} (approximately 0.31% y^{-1}) (Fig. 3). For seed Zn content ($r^2 = 0.65$), the mean decrease was approximately 0.10 µg g^{-1} y^{-1} (0.36% y^{-1}). At the Manhattan location, seed Zn content ($P < 0.05$, $r^2 = 0.29$) exhibited a mean decrease of approximately 0.05 µg g^{-1} y^{-1} (0.16% y^{-1}) (Fig. 3). Also at Manhattan, seed Se content exhibited a significant regression ($P < 0.01$) on date of variety release. The r^2 in this instance was 0.45, with a mean decrease in seed Se content of 0.12 ng g^{-1} y^{-1} (0.23% y^{-1}) (Fig. 3). It should be noted that while regression of seed Se content on year of release was not significant at Hutchinson, removal of one potential outlier value (variety 2137) results in a significant regression ($P < 0.005$), a large r^2 value (0.60), and a corresponding calculated mean decrease in Se of $1.7\,\text{ng}\,\text{g}^{-1}\,\text{y}^{-1}$ (0.38% y^{-1}).

DISCUSSION

Major advances in wheat improvement have focused on increasing yield and improving end-use properties. Productivity has increased dramatically due to genetic modification of traits such as growth habit, disease resistance, and improved adaptation, as well as the influence of improved crop management practices.[7] While increasing productivity of wheat is a well-documented success, the relationship between increased productivity and seed micronutrient content is less well understood. It is important to determine if improved yields may be exacerbating micronutrient malnutrition in humans due to a reduction in wheat seed micronutrient concentrations. Further, if efforts are to be undertaken to develop micronutrient-enriched staple crops such as wheat, understanding relationships between advances in wheat productivity and seed micronutrient concentrations will provide insights into possible obstacles that may be encountered.

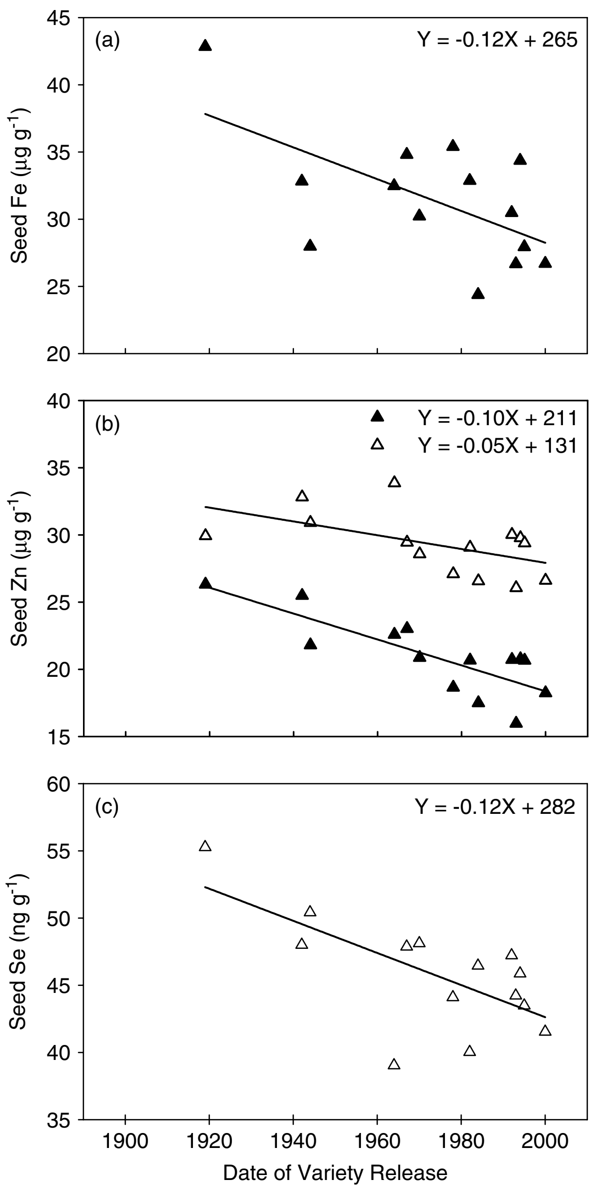

Figure 3. Significant regressions of wheat seed micronutrient contents on date of variety release. Filled and open triangles are data points for Hutchinson and Manhattan, KS, respectively. The best-fit simple linear regression line is shown.

In the USA, approximately 64 kg of wheat per capita is consumed annually, making it the most important cereal grain in US consumer diets.[2] Of this, the main class is HRWW. The history of US HRWW production and improvement is well documented, and thus it serves as a useful model for examining for shifts in seed micronutrient concentrations in wheat during the course of decades of genetic improvement, which have resulted in yield gains averaging approximately 1% per year.[15] In this study, we examined the mineral micronutrient concentrations of 14 HRWW varieties released and grown in the USA during a period of time spanning over a century. The varieties included the landmark HRWW variety Turkey, which was introduced to the USA in the late 1800s and was an important HRWW for decades, and varieties representing the result of wheat breeding efforts and date from the early 1940s to the late 1990s. While variation in mineral element concentration in wheat has been reported previously,[19–23] to our knowledge this is the first study to examine the impact that decades of genetic improvement of yield have had on seed micronutrient concentrations in wheat.

Significant location effects on wheat seed mineral concentrations were detected in this study, as has been reported for a single wheat variety.[19] Interestingly, in our study the rankings of varieties for seed Fe and Zn, and to a lesser degree Cu concentration, were found to be similar between locations. The concordance between relative rank in seed micronutrient concentrations between wheat genotypes at the two locations suggests not only an underlying genetic basis to the variation, but also limited genotype–environment interaction for these traits. The apparent reduced genotype–environment interaction in the newer varieties may reflect greater within-cultivar genetic homogeneity, since older wheat varieties tend to be less genetically homogeneous due to differences in breeding methodologies. While this study permitted us to examine genotype–environment interactions where 'environment' is a different geographic location, it will be important in future studies to assess the effect of genotype–environment interactions where 'environment' is defined by different years at the same location. This will provide additional important information on year-to-year stability in genotype rankings for micronutrient accumulation in the grain.

The interlocation correlation results for Fe, Zn, and Cu contrasted greatly with those for seed Se

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content, for which there was no apparent congruence in ranking between locations. However, unlike the other three elements, Se is not essential for plants and thus its accumulation is not expected to be specifically regulated *per se* by the plant as is the case for the other minerals examined.[24] It is recognized that the Se content of plant tissues is largely a reflection of the soil Se content.[25] Therefore, the eightfold difference in mean seed Se concentrations between the two locations is thus likely to reflect differential abundance of Se in the soil at the two locations.

While variation between genotypes for seed Zn and Cu concentrations has been reported previously in English wheat,[20] the seed did not come from controlled trials and so the differences detected likely included the influence of non-genetic factors. In the present study, seeds of varieties came from replicated trials,[16] allowing us to detect genetic variation among the evaluated HRWW genotypes for seed Fe, Zn, Cu, and Se concentration. It is clear that the extent of variation in seed micronutrient content between varieties can vary dramatically depending on the location. In this study, the most extensive differences between varieties for micronutrient content were identified at the location that exhibited high mean yields and large yield differences between varieties.[16]

The potential relationship between changes in seed micronutrient concentrations and genetic improvement of yield was a particular focus of this study. Regression analysis indicated that for two micronutrients (Fe and Zn) a negative relationship between seed micronutrient content and yield was present. However, Zn was the only one of these that displayed a significant negative relationship with yield at both of the locations. A comparable analysis undertaken with year of release serving as the independent variable provided results similar to those from the regression of seed micronutrient content on yield. This is expected since yield has steadily increased over time.[16] However, in contrast to the results of the yield regressions, at one location a negative relationship between seed Se content and variety age was detected, with a similar result obtained at the other location when a potential outlier was removed. Taken together, the results of both regression analyses suggest that breeding for increased yield in HRWW has had a negative effect on seed Fe, Zn and Se concentrations. However, the magnitude of this effect is influenced by the location at which the plants are grown. For those micronutrients that exhibited a significant regression of seed content on variety age, the mean annual percent decrease ranged from 0.16% y^{-1} to 0.38% y^{-1}, depending both on the mineral and the location. Over the course of several decades, this represents a significant effect that, if continued, will further erode the seed mineral content in wheat.

The basis of the negative relationship between increased yield and reduced seed micronutrient content may be multifactorial. Ostensibly, higher yields could magnify varietal differences in seed micronutrient concentrations if total shoot micronutrient accumulation is similar between varieties, but is partitioned to differing amounts of seed mass. Indeed, there has been strong selection for increased seed mass as a proportion of the above-ground portion of the plant in HRWW.[16] It should be noted that kernel weight was reported not to differ among these varieties in the earlier study,[16] and thus dilution due to increased kernel volume does not appear to be a contributing factor to our results.

This study demonstrates that within the US HRWW gene pool the modern era of breeding and the resultant genetic improvement of yield has, in some instances, also ushered in shifts toward reduced seed mineral micronutrient concentrations. This trend may not be manifested at all locations, nor for all micronutrients. Nonetheless, the detection of clear negative relationships between yield and certain mineral micronutrient concentrations at one or both locations examined here indicates that efforts to breed for increased seed mineral micronutrient concentrations must take into consideration this relationship. In many crops, inverse relationships between important characters are commonly encountered. For instance, yield and protein content in wheat often exhibit an inverse relationship,[26] as do yield and oil content in soybean.[27] However, progress in improving characters that exhibit such inverse relationships is still possible. To increase seed mineral micronutrient concentrations, high-yielding genotypes that do not display low mineral levels would be extremely valuable. In our study of a limited number of varieties, significant differences in seed micronutrient concentrations were detected between some of the newer genotypes. Thus, even though negative associations between yield and seed mineral micronutrient content can occur, it should be possible to develop wheat that is both high yielding and possesses increased seed mineral micronutrient content.

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