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A Field-Based Analysis of Genetic Improvement for Grain Yield in Winter Wheat Cultivars Developed in the US Central Plains from 1992 to 2014

Trevor W. Rife, Robert A. Graybosch, and Jesse A. Poland*

ABSTRACT

Progress in plant breeding programs is the result of creating and selecting new lines with novel allele combinations that perform better than their parents. This year-on-year improvement is known as genetic gain and is a function of genetic diversity, selection accuracy, selection intensity, and selection cycle time. To estimate the gain in wheat (*Triticum aestivum* L.) breeding in the US Central Plains, lines that were submitted to the collaborative Southern Regional Performance Nursery (SRPN) between 1992 and 2014 were grown in a common nursery for 3 yr at two locations in a single-replicate augmented block design. Moderate to high broad-sense heritability was observed for plant height ($H^2 = 0.88$), heading date ($H^2 = 0.79$), and grain yield ($H^2 = 0.41$). From the common grow-out, genetic gain for yield over the time period was estimated at 1.1% yr⁻¹, whereas individual breeding program genetic gain varied between 0.3 and 1.9% yr⁻¹. Increases in Kansas state on-farm yields during the same period showed a nonsignificant trend of 0.13% yr⁻¹ with large year-to-year variation. These results suggest that although progress is being made in US Central Plains breeding programs, a yield gap remains that could be attributable to genetic progress not being realized in on-farm production.

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Abbreviations: BLUE, best linear unbiased estimate; i.i.d., independent and identically distributed; SRPN, Southern Regional Performance Nursery.

GENETIC GAIN, or the year-on-year progress observed in plant breeding, is the benchmark by which plant breeding programs show advancement and is a function of genetic diversity, selection accuracy, selection intensity, and selection cycle time. An assessment of the rate of genetic gain within and across breeding programs gives a benchmark for progress in plant breeding. With accelerating population growth, decreasing arable land, and climate change, the necessary rate of genetic gain to meet future food demand is estimated at 2% or higher (Ray et al., 2013). Measuring the current rate of genetic gain in breeding programs is one of the most important assessments for tracking the progress toward the goal of global food security in the coming decades.

Assessment of long-term genetic gain can be conducted using year-on-year evaluations from a breeding program or from collaborative testing sites (Schmidt and Worrall, 1983; Graybosch and Peterson, 2010). To assist with the important multilocation evaluation needed for final cultivar release, collaborative regional testing networks across the United States have been in place for >80 yr and represent a vast resource of the best, near-release cultivars and breeding lines for a generational study. The Hard Winter Wheat Regional Nursery Program was established in 1931 by

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the USDA-ARS to measure performance, quality, disease resistance, and other agronomic traits of near-release wheat (*Triticum aestivum* L.) cultivars from breeding programs in the US Central Plains. Entries submitted by breeders in the region are evaluated at >30 locations along with multiple, common, long-term check cultivars. This nursery has been regularly used to estimate genetic gain over time relative to Kharkof, a tall check cultivar (Schmidt and Worrall, 1983; Graybosch and Peterson, 2010; Graybosch and Peterson, 2012).

Previous estimates for genetic gain across the same region have reported varying improvement. Battenfield et al. (2013) provided a good review of global studies measuring genetic gain, with estimated gain in the Great Plains at 0.40% yr⁻¹ relative to the performance of TAM 101, a common check cultivar. Cox et al. (1988), using 30 cultivars that were released throughout the 20th century, found a 1% yr⁻¹ increase. Graybosch and Peterson (2010) examined genetic gain for a broad period (1959–2008) as well as for a shorter, more recent period (1984–2008). Gain was reported as 1.1% yr⁻¹ increase over Kharkof, the common check cultivar for the entire time period, but this trend was nonsignificant for more recent years (Graybosch and Peterson, 2010). Investigating the idea that specific adaptation from individual breeding programs may have led to a current plateau of genetic gain, Graybosch and Peterson (2012) examined yield gains in predetermined growing regions, again finding a lack of gain in the Southern Regional Performance Nursery (SRPN), except for where the check cultivar was poorly adapted. Understandably, this gives some credence to the ideas originally presented by Schmidt (1984) of a slowdown or plateau of genetic gain in recent decades.

However, many of these previous studies have been retrospective and relative since they use the unbalanced regional nursery data across years and rely on the transformation of the mean entry yield into a relative percentage of the yield of a long-term check. This approach assumes minimal genotype × environment interaction, particularly for the long-term check. This assumption is likely not satisfied for the SRPN since the long-term check, Kharkof, is a tall cultivar, in contrast with all contemporary wheat cultivars being semidwarf. Kharkof is also better adapted to cooler environments but is still used for comparison in warm and dry environments of the Southern Plains (Graybosch and Peterson, 2012). Further complicating pre-1998 historical measures of genetic gain for the SRPN: each participating location previously maintained their own source of Kharkof, presenting an opportunity for genetic drift and selection, resulting in subsequent phenological and morphological differences (Cox and Worrall, 1987). Other studies have examined genetic gain in wheat in the United States using a common nursery experiment but have evaluated a relatively small number of cultivars ($n =$

12–35) representing a large number of years (average 3.8 yr entry⁻¹) and have found varying amounts of genetic gain (0.40–1.4%) (Cox et al., 1988; Donmez et al., 2001; Khalil et al., 2002; Fufa et al., 2005; Battenfield et al., 2013).

To reduce the confounding issues detailed above and determine an estimate for genetic gain of wheat breeding in the US Central Plains, 711 entries that were evaluated in the SRPN from 1992 to 2014 were grown in common garden experiments for a total of four site-year combinations. Phenotypic measurements for height, heading date, and grain yield were collected. Genetic gain from 1992 to 2014 was estimated across the entire collection of entries, as well as on a breeding program basis. To determine the extent to which this gain has been realized in growers' fields, the rate of gain in on-farm yields over the same period was determined. A lack of realized yield could indicate that progress in on-farm yields has not matched the progress from breeding programs or could show that genetic "gain" in wheat breeding for this region has primarily been maintenance breeding or the prevention of yield loss attributable to increasing pathogen pressure and less favorable environments. There are stark implications of reduced gain, an observable yield gap, and the effect it will have on future productivity and food security.

MATERIALS AND METHODS

Plant Material

Seed was acquired from original samples distributed by the SRPN for entries dating back to 1992. Entries were grown in a greenhouse in fall 2012 to increase the amount of seed and then grown in single rows in summer 2013 at the Kansas State University Ashland Bottoms Research Farm (39.131891° N, 96.61981° W) to further increase the amount of seed and allow for replicated testing. For subsequent field trials, 711 entries were chosen based on seed availability and limiting redundancy (Supplemental Table S1).

Field Design and Data Collection

An augmented block design with two regional check cultivars ('Everest' and 'TAM 112') was created using the agricolae package in R with ranges corresponding to blocks (de Mendiburu, 2013). Experimental entries were randomly assigned to a block for each environment (location-year combination). Entries were tested for 3 yr (2014, 2015, and 2016) at Ashland Bottoms Research Farm near Manhattan, KS (39.132364° N, 96.620462° W) and the Agricultural Research Center in Hays, KS (38.850236° N, 99.339827° W), giving six location-years of evaluation. Trials evaluated at Ashland bottoms were treated with Nexicor fungicide to reduce biotic stress that could affect phenotypic measurements. In this study, location-years are referenced by the last two digits of the year and first letter of the location (A = Ashland, H = Hays; e.g., 14A, 15H).

Entries were evaluated in 0.75-m × 2.44-m three-row plots in 14A, 14H, and 15A trials due to limited field space availability, and in 1.5-m × 2.44-m six-row plots for 15H, 16A, and 16H trials. Yield was collected from 14A, 15A, 15H, and 16H,

with the other two trials being lost because of drought (14H) and flooding (16A). The Field Book app was used to collect the following agronomic traits commonly collected within breeding programs: height from 15A and 16H, and heading date from 14A and 15A (Rife and Poland, 2014).

Data Analysis

Twenty entries that were originally submitted to the SRPN as hybrids were removed from subsequent analysis. Plots that had seed loss or mixing resulting from harvesting errors were removed from additional analysis (11 in 14A, 10 in 15A). No data were collected or used for analysis from the two trials that were lost (14H and 16A). Plot-level yields were normalized based on plot size. Entry yield in each environment was adjusted using the checks within each block. The grand mean of the check cultivars in each environment was used to calculate a block adjustment factor that was used to modify the yield for each entry in the block.

To estimate variance components, a linear mixed model was fit for each trait using the lmer function from the lme4 package in R (Bates et al., 2014). Variance components were used to calculate broad-sense heritability as follows:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_{err}^2}{e}} \quad [1]$$

where σ_g^2 is the genotypic variance, σ_{ge}^2 is the genotype \times environment interaction variance, σ_{err}^2 is the residual error variance, and e is the number of environments (Holland et al., 2010).

Genetic Gain

A linear mixed model was fit using the lme4 package in R (Bates et al., 2014) for adjusted yield as follows:

$$y_{ijk} = \mu + g_i + m_j + r_k + gm_{ij} + gr_{ik} + e_{ijk} \quad [2]$$

where y_{ijk} is the yield adjusted for plot size, μ is the overall mean, g_i is the fixed genotype effect for each genotype, m_j is the random effect for each j th year that is independent and identically distributed (i.i.d.) $m_j \sim N(0, \sigma_j^2)$, r_k is the random effect for each k th location that is i.i.d. $r_k \sim N(0, \sigma_k^2)$, gm_{ij} is the random interaction effect of the i th genotype and j th year that is i.i.d. $gm_{ij} \sim N(0, \sigma_{ij}^2)$, gr_{ik} is the random interaction effect of the i th genotype with the k th location that is i.i.d. $gr_{ik} \sim N(0, \sigma_{ik}^2)$, and e_{ijk} as the random error assumed i.i.d. $e_{ijk} \sim N(0, \sigma_e^2)$. Best linear unbiased estimates (BLUEs) were extracted from the model using the coef function in R (R Core Team, 2017). The BLUE for each entry was assigned to the year the entry was first evaluated in the SRPN and a linear model was fit, with BLUEs as a function of the evaluation year.

Genetic gain within each breeding program was calculated by subsetting the BLUEs by program and refitting the linear model above. Programs with <20 entries evaluated in this study were excluded from individual program assessment.

Kansas Yield Data

Kansas statewide yield data, in bushels per acre, from 1903 to 2015 were obtained from the USDA National Agricultural

Statistics Service (USDA-NASS, 2016). Genetic gain over time was measured by fitting independent linear models with yield (in tons hectare⁻¹) for the following time periods: 1903 to 1960 (tall wheat), 1961 to 1980 (semidwarf transitional period), 1981 to 2015 (semidwarf wheat), 1961 to 2014 (modern era semidwarf wheat), and 1992 to 2014 (representative years used in this study).

RESULTS AND DISCUSSION

Phenotypic Data

Of the four nurseries that were harvested (14A, 15A, 15H, and 16H), 3092 plots were planted, and 2991 plots were used in this analysis, with a total of 10,911 phenotypic measurements collected for yield, height, and heading date (Table 1). Across this set of nurseries, moderate to high heritability was observed for height ($H^2 = 0.78$), heading date ($H^2 = 0.79$), and yield ($H^2 = 0.45$). These estimates are in line with similar studies from the same region (Häberle et al., 2007; Zhang et al., 2015).

There was a small, negative, nonsignificant relationship observed between height and year of evaluation ($r = -0.04$, $p = 0.25$). A small, though significant, negative correlation was also observed between heading date and year of evaluation ($r = -0.083$, $p < 0.05$). Although broad conclusions are difficult to determine from the limited environments observed in this study, the lack of relationship between original year of evaluation and these two agronomic traits could suggest that fundamental agronomic characteristics within Central Plains wheat breeding programs have reached an optimum and are no longer under strong directional selection.

Breeding programs fundamentally rely on viable environments for evaluation, and therefore a barrier to progress in any breeding program is environments that are severely impacted by extreme weather conditions. Even in this limited experiment, one-third of the trials were lost, demonstrating how difficult plant breeding can be in a region with large environmental variability. With wheat breeders in the central plains losing a substantial number of their field trials in any given year, it is an understandable and considerable challenge to generate progress in this target region.

Genetic Gain

Measuring genetic gain is useful to understand the amount of progress that has been made in plant breeding

Table 1. Summary of phenotypic data collected with 95% confidence intervals: adjusted and normalized plot yield, height mean, and days after 1 January to heading mean.

Environment	Plot type	Adjusted yield kg	Height cm	Heading date
14A	3-row	1.77 ± 0.25	–	129.5 ± 0.15
15A	3-row	1.66 ± 0.25	85.68 ± 0.56	124.6 ± 0.15
15H	6-row	1.18 ± 0.28	–	–
16H	6-row	1.90 ± 0.40	87.17 ± 0.54	–

programs. Genetic gain from this collection of entries was an estimated 1.1% yr⁻¹ (95% confidence interval = 0.9–1.29%, Fig. 1). Comparatively, this figure is higher than other measures of genetic gain in studies that were examined in similar time periods (Graybosch and Peterson, 2010, 2012). Substantial variability was observed for yield within each year of origin.

Although the calculated gain was higher than that reported in other studies, it is difficult to determine if this gain was attributable to improved yield potential or depressed yields for older cultivars, potentially due to new biotic stresses (e.g., new pathogen races). So-called “maintenance breeding” that keeps the most recent cultivar yield at a certain threshold in response to recent biotic and abiotic stresses could potentially be responsible for the observed gain. Supporting this idea, 2016, the evaluation year that showed the strongest year-of-entry trend among the lines evaluated also had increased biotic pressure from stripe rust (*Puccinia striiformis*) and leaf rust (*Puccinia triticina*) contributing to yield loss in older cultivars.

To evaluate the progress that has been made within each program, entries were divided into subsets by program-of-origin and gain was recalculated. There was substantial variation in gain across different breeding programs. Gain within individual programs ranged from 0.37 to 1.92% yr⁻¹ (Fig. 2, Supplemental Table S1). Because of the relatively few number of lines representing each program, large confidence intervals around the percent gain estimates were observed for nearly every program and broad conclusions about individual programs or program-to-program comparisons cannot and should not be made.

Multiple breeding targets may be responsible for some of the genetic gain variation observed between breeding programs. For instance, Oklahoma State University selects wheat cultivars for high grain yield but also focuses on developing wheat cultivars that produce substantial winter forage, often resulting in a yield tradeoff. The combination of breeding lines from the same program but with contrasting breeding targets creates the possibility of limiting genetic gain for the breeding program as a whole in the target environments evaluated for this study.

Other potential explanations for variation in the genetic gain among breeding programs include the primary target of each breeding program and submission of subsets by breeders. Breeding programs with primary selection sites more closely related to the testing sites used for evaluation in this study would be more likely to overperform relative to those selected in for different target environments. Breeders may also be selective in the entries submitted to this nursery. For example, the northernmost breeding program at the University of Nebraska tends to submit lines with early maturity to the SRPN, reserving different elite lines with later maturity for the Northern Regional Performance Nursery.

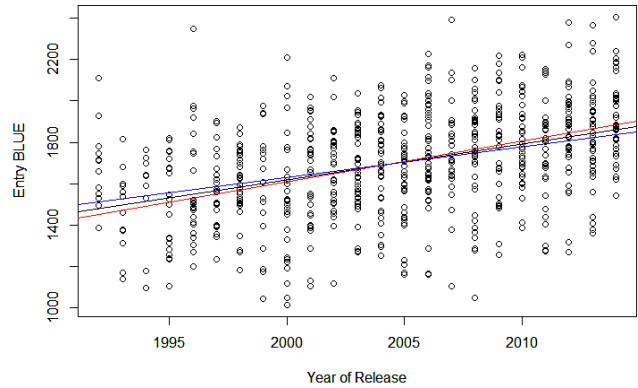


Fig. 1. Best linear unbiased estimates (BLUEs) of entries plotted against the year they were first evaluated in the Southern Regional Performance Nursery. The black line indicates linear regression of entry BLUE on year of release (slope = 17.25). Red and blue lines indicate the 95% confidence interval around the regression line.

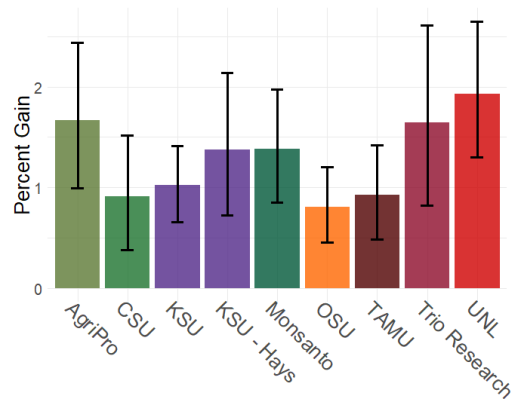


Fig. 2. Estimated genetic gain in percentage per year for individual breeding programs contributing entries to the US Winter Wheat Southern Regional Performance Nursery. The 95% confidence interval of the individual estimates is marked by error bars. Breeding programs measured were AgriPro, Colorado State University (CSU), Kansas State University (KSU), Kansas State University–Hays (KSU–Hays), Monsanto, Oklahoma State University (OSU), Texas A&M University (TAMU), Trio Research, and University of Nebraska–Lincoln (UNL).

On-Farm Yields

Although the ultimate goal for a breeder is successfully developing experimental lines and cultivars that perform significantly better than the most widespread cultivars in the area, the success of a new cultivar, and the plant breeding enterprise as a whole, is the transfer of genetic gains made within a breeding program to increased farm yield. To evaluate the extent to which genetic gain has been transferred from breeding programs to farmers, data from Kansas statewide yields from 1903 through 2015 were used to calculate the mean yield increase per year across several different time periods. Time periods were chosen based on years with similar agronomic practices and germplasm. The five different time periods for which yield gain was calculated were 1903 to 1960, corresponding to tall wheat cultivars with less intense wheat

breeding and agronomic management; 1961 to 1980, corresponding to the introduction of semidwarf wheat cultivars and increased N application; 1981 to 2015, corresponding to contemporary breeding and complete adoption of semidwarf cultivars; 1961 to 2015, corresponding to the totality of what can be considered the modern breeding era; and 1992 to 2014, corresponding to the years used in this study. A linear model was used to estimate the amount of gain in each time period (Fig. 3).

There were substantially different yield gains during these different time periods, roughly corresponding to the implementation and exploitation of different agronomic and genetic technologies. The period relating to increasing adoption of semidwarf cultivars and more applied N had substantially more gain than any other evaluated period. Dividing the period since the introduction of semidwarf cultivars into several intervals indicates that yield gains on farm are decelerating. This could be attributable to a number of factors including disease pressure, environmental stresses (Lobell et al., 2011), implementation of agricultural practices such as no-till, agricultural intensification, or factors related to a changing climate.

Of interest is the fact that when evaluating modern wheat cultivars as a single time period (i.e., 1961–2015), the rate of gain is in line with the generally accepted 1% yr⁻¹ (Tester and Langridge, 2010; Battenfield et al., 2013). However, this estimate is misleading and innately attributable to the inclusion of the extreme growth of on-farm yields from 1961 to 1980. The period corresponding to the years used in this study had the least amount of gain in on-farm yield (0.13%), indicating a gap between the rate of genetic improvement in breeding programs and the realization of the improved yield potential in growers' fields. However, it is important to consider that large year-to-year variations in yield (e.g., 2014 with severe drought or 2016 with record yield) can considerably affect the precision of determining the true gap between breeding and on-farm yields and subsequent inferences.

Much work has been done to quantify the current rate of genetic gain, as well as to estimate the rate necessary to sustain current trends in population growth and meet projected food demand (Tester and Langridge, 2010). The current accepted perspective is that we must significantly increase progress relative to the historical rate of gain, and in many situations, we need to double the rate of gain (Tester and Langridge, 2010; Ray et al., 2013). However, this conclusion is based on the idea that the current rate of genetic gain is a continuation of the significant increases that were seen during the transitional period to semidwarf wheat, which is clearly not the case. Although we found gain to be positive in both experimental and on-farm environments, the proportional increase seen in the on-farm yields during the period of interest highlights a potential gap between increased breeding productivity

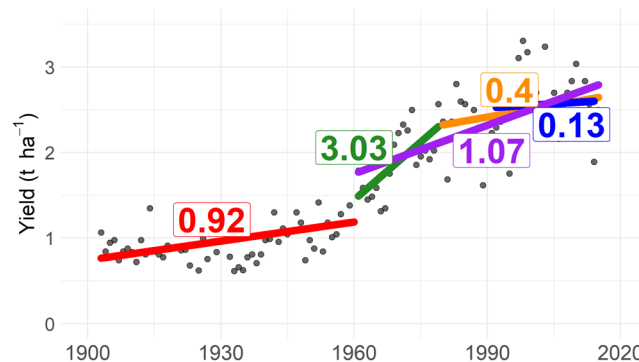


Fig. 3. Kansas on-farm yield trends for 1903–1960 (red), 1961–1980 (green), 1981–2015 (orange), 1961–2015 (purple), and 1992–2014 (blue), with percentage gain estimates noted in the respective boxes.

and the realization of those genetic gains on farmers' fields. In contrast with the initial decades of growing new semidwarf varieties when the gains were substantial, there have been nominal gains experienced during contemporary breeding, and these have been more slowly realized by farmers. New genetic or technological enhancements will be necessary to improve this current trend.

Conflict of Interest

The authors declare that there is no conflict of interest.

Supplemental Material Available

Supplemental material is available online for this article.

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