Physiological Changes Across Historical Sorghum Hybrids Released During the Last Six Decades

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Summary
For the last decades, sorghum (Sorghum bicolor L. Moench) improvement in the United States (US) has been related to targeted modifications in genotype, environment, and management (G × E × M) combinations. Retrospective studies are relevant to document changes in the phenotype associated to breeding process and to explore alternatives to improve yield and its physiological associated traits. This study aims to characterize yield changes over time for hybrids with different years of release. Field trials were conducted during 2018 and 2019 growing seasons in eight environments/site-years across the states of Kansas and Texas including 20 grain sorghum hybrids released between 1963 and 2017. Grain yield was measured across all hybrids and environments. Detailed physiological descriptors were measured in one of the environments including grain filling, grain set efficiency (grains g-1) at flowering, panicle length, and dynamics of water-soluble carbohydrates (WSC) during the reproductive period. Overall sorghum grain yield improvement was 0.4 bu/a/year (P < 0.005). Grain set per unit of reproductive biomass at flowering was positively associated with the hybrid’s year of release, explaining the increases in grain number. Panicle size increased in newer hybrids, thus, supporting the reported changes in grain number per unit area. Modern sorghum hybrids displayed greater WSC remobilization during the reproductive period (P < 0.05). However, further research on sorghum’s WSC dynamics is needed for understanding its contribution to yield improvement.

Introduction
Sorghum (Sorghum bicolor L. Moench) is an important cereal crop ranking in production among the top five cereal crops of the US, its major producer (Maunder, 2002). During the last decades, improvement of grain sorghum yield in the US has been mainly related to changes in G × E × M combinations (Assefa and Staggenborg, 2010; Pfeiffer et al., 2018). However, physiological changes related to sorghum hybrids released since 1960s until the present decade remains to be determined.

Yield gains and related traits have been studied in detail on other cereal crops such as wheat and maize. Donmez et al. (2001) and Xiao et al. (2012) suggested that the understanding of the physiological traits associated with yield formation plays a key

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role in the identification of limiting factors, and the development of new strategies for yield improvement in winter wheat. Similarly, plant traits associated with yield genetic gain over time in maize have been thoroughly studied in US hybrids (Duvick, 2005), accounting for approximately 50% of the yield gain during the past seven decades. Comparatively, yield improvement in grain sorghum can be assumed to be around 40% due to hybrid improvement and around 60% due to management (Duvick, 1999).

Highlighting the importance of identifying traits associated with yield improvement, this study proposes to characterize the yield and physiological trait changes over time for sorghum hybrids with different years of release. The lack of information on US sorghum yield changes over time motivated us to pursue the implementation of this research study. Our hypothesis is that there has been genetic gain for yield in Pioneer sorghum over the last 60 years due to changes in a few key traits related to resource capture and resource use efficiency.

**Procedures**

A total of eight field experiments were conducted across the states of Kansas and Texas during the 2018 and 2019 growing seasons (four trials each season). During 2018, experiments were planted in the following counties: Cloud (KS), Finney (KS), Riley (KS), and Moore (TX). For the 2019 planting season, experiments were conducted in the following counties: Riley (KS), Moore (TX), Hale (TX), and Dallam (TX). Table 1 presents a summary of climatic conditions during 2018 and 2019 growing seasons.

The experimental design for all locations was a randomized complete block design (RCBD), with 20 genotypes and three replications. Sorghum genotypes were Pioneer hybrids spanning six decades of genetic selection (from 1963 until 2017). Plots were 17.5-ft long per two rows (30-in. row spacing across all sites) for all the locations except Riley, KS (2019) with 8 rows and 17.5-ft long. All locations were utilized to obtain data on sorghum yield, and one location (Riley, KS, 2019 season) was used to obtain detailed physiological descriptors of yield formation.

**Measurements**

Total aboveground plant biomass was measured at flowering and maturity. Plant fractions were separated in leaves and stem during vegetative stages; and leaves, stem, and panicle (plus grain) during the reproductive stages. Dry weight was obtained after drying plant fractions in a forced-air oven at 150°F until constant weight.

Grain dry matter and moisture content were collected during the grain filling period and at maturity.

Grain set efficiency was calculated with the relationship between the number of grains per panicle and the panicle dry weight at flowering.

\[
\text{Grain set efficiency} = \frac{\text{Grain number}}{\text{Panicle biomass}}
\]
where grain number is the final grain number in grains per ft$^2$ and panicle biomass is the panicle dry weight at flowering in grams per ft$^2$.

Pictures of ten consecutive panicles per plot with metric reference were taken at physiological maturity to determine panicle length, compiling a total of 30 panicle measurements per hybrid. Panicle length is defined as the length in inches of the panicle from the first branch to the top of the panicle.

Water soluble carbohydrates (WSC) were analyzed in the stem fraction using the anthrone reagent method (Yemm and Willis, 1954).

**Results**

**Yield Across Years of Release and Yield Components**

A significant increase in yield across decades has been found for the evaluated sorghum hybrids released from 1963 until 2017 across the eight environments evaluated. The yield trend across years was represented in Figure 1A using the best linear unbiased estimators (BLUEs) for grain yield on each genotype. Yield gain was primarily associated with a greater number of grains per unit area across time (Figure 1B) rather than improvements in grain weight (Figure 1C), although this component remained relatively stable over time. Similar responses on yield and its components were previously documented by Assefa and Staggenborg (2010) and Pfeiffer et al. (2018) for sorghum hybrids in the US.

**Grain Set Efficiency and Panicle Size Over Years of Release**

A positive relationship was found between grain set efficiency and the period of years of introduction of the selected hybrids (Figure 2). Hybrids with greater yield are able to set more grains per unit of reproductive biomass at flowering (Gizzi and Gambin, 2016). In parallel, an increase of the size of the panicle was documented across years (Figure 3) contributing to the explanation of an increase in the number of grains per panicle. These results are consistent with findings documented by Pfeiffer et al. (2018), reporting an increase in panicle size for US sorghum hybrids.

**Grain Number as a Function of WSC Concentration and Remobilization**

The concentration of carbohydrates (WSC) at flowering was not significantly associated with the number of grains (Figure 4A). However, a positive relationship was found between the number of grains and the remobilization of WSC from stems during the reproductive period (Figure 4B). Modern sorghum hybrids were able to fill a greater number of grains per unit of area by increasing the remobilization of WSC from the stems during the reproductive period. Likewise, Pfeiffer et al. (2018) found in new hybrids less sucrose (%) in the biomass at maturity as an indicator of more use efficiency of the assimilates accumulated during the vegetative period.

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| Table 1. Weather information for 2018 and 2019 growing season for Cloud (KS), Dallam (TX), Finney (KS), Hale (TX), Moore (TX), and Riley (KS) locations |
|---------------------------------------------------------------|
| Location | 2018 | 2019 | 2019 |
| Max. Temp. (°F) | 76.3 | 83.6 | 78.4 | 79.2 | 76.8 | 88.9 | 88.5 | 80.2 |
| Min. Temp. (°F) | 53.8 | 57.0 | 52.1 | 57.2 | 54.5 | 55.6 | 66.1 | 58.8 |
| Precipitation (in.) | 22.1 | 19.5 | 4.45 | 26.4 | 12.2 | 5.46 | 11.4 | 26.7 |

The minimum and maximum temperatures (Min. Temp. and Max. Temp., respectively) are the averages of minimum and maximum temperatures per day from planting to harvest for each site × year in Fahrenheit degrees (°F), respectively. The precipitation represents the accumulated rainfall from planting to harvest for all locations in inches. (Kansas Mesonet, 2017; TexMesonet, 2017).
Figure 1. Relationship between best linear unbiased estimators (BLUEs) for grain yield (A), grain number (B), and grain weight (C) all relative to the year of release (from 1960s to 2010s) for 2018 and 2019 experiments.

Figure 2. Relationship between grain set efficiency (grain number/panicle dry weight) and years of release of the hybrids (from 1960s to 2010s) for the 2018 and 2019 experiments.
Figure 3. Correlation between means of panicle length (expressed in inches) and years of release of the hybrids (from 1960s to 2010s) for the 2019 experiment.

Figure 4. Grain number per unit area as a function of water-soluble carbohydrates (WSC) at flowering (A) and WSC remobilization (WSC at flowering - WSC at maturity) (B) for the 2018 experiment.