

Historical Characterization of Sorghum Grain Filling Dynamics

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Summary

Understanding crop response to manipulations in source (number of leaves) and sink (panicle) during the growing season provides useful information to develop crop breeding strategies. In the present study, we assessed how source-sink manipulation can affect sorghum (*Sorghum bicolor* L.) yield and its components—grain number and grain weight (including grain filling dynamics)—for hybrids released in the past 60 years. The field experiment was conducted during the 2021 growing season in Wamego, KS (US), testing six commercially available grain sorghum hybrids released between 1963 and 2020. Grain weight significantly decreased from 28 to 21 mg in defoliation treatments among hybrids over time; and reached a maximum value of 34 mg when panicles were halved ($P < 0.05$). For the control scenario, yield consistently increased over time ($P < 0.01$). When source-sink treatments were applied, there was a reduction of 33 bu/a for the defoliation and 39 bu/a for the panicle halving ($P < 0.001$). Regarding grain number per unit area, the trend was similar across hybrids over time ($P < 0.1$) but decreased with the panicle halving to 1600 grains on average ($P < 0.001$) relative to both control and defoliation scenarios. Over time and across source-sink treatments, there was no significant change in grain filling rate. However, a significant reduction for the duration of the grain filling was documented for defoliated plants, with a greater decrease over time.

Introduction

Grain sorghum (*Sorghum bicolor* L.) is the fifth-largest cereal crop in the world (Ciampitti and Prasad, 2019), standing out for competitive advantages including high biomass production, grain quality, and yield stability under stress conditions such as drought and high temperatures (Gizzi and Gambin, 2016). Although sorghum possesses these desirable plant traits, the genetic gain in the past decades has been low compared to other crops. For example, whereas for maize the yield genetic gain increased 54-88 kg/ha (0.87-1.27 bu/a) per year (Fernández et al., 2022), for sorghum it was only 19-35 kg/ha (0.30-0.55 bu/a) per year (Demarco et al., 2021). Therefore, a better understanding of the source-sink balance for sorghum would help to develop breeding strategies to improve marketability in current production systems.

Previous studies on source-sink relationships provided evidence that crops could be yield-limited by source, sink, or both (Borras et al., 2004). In this context, source refers to photosynthesis capacity of green leaves, and sink refers to the growing capacity of organs (e.g., grain number and grain size) to accumulate assimilates (critical for yield

formation). The rates and amounts of dry matter accumulation and the growth of harvestable organs of a crop are determined by the assimilate supply of green leaves (source strength) and the capacity of organs to store assimilates (sink strength) (Asseng et al., 2016).

This study was conducted to characterize yield and its components in response to manipulations on the source-sink ratio for sorghum hybrids with different years of release to identify plant traits associated with yield improvement.

Procedures

The study was conducted at the Corteva Agriscience research station in Wamego, KS (US), during the 2021 growing season. Six sorghum hybrids from Corteva Agriscience were selected to represent six decades of genetic selection (from 1960 until 2020).

Sorghum was planted on June 7, 2021, in eight-row plots. Each row length was 16 ft with 30-in. row spacing.

Standard agronomic practices were followed to maintain the field free of weeds, pests, and diseases during the season. The experimental design was a split-plot with factorial subplot structure. Hybrids were assigned to whole plots, and source-sink treatment factor was assigned to each sub-plot ten days after flowering. Three levels of source-sink ratio were included: 1) control; 2) increase of the source-sink ratio by halving the panicle along the rachis; and 3) reduction of the source-sink ratio by partially removing leaves.

To increase the source-sink ratio (treatment 2), all the branches from one side of the panicle were manually removed; with the expectation to remove 50% of the grains with a uniform distribution across the four panicle positions. To decrease the source-sink ratio (treatment 3), defoliation was accomplished by removing 80% of the leaves of each plant treated (Heiniger et al., 1993).

During the grain filling period, one panicle per plot and sub-plot was collected to characterize the seasonal dynamics of grain dry weight. In each of these plants, phenology was tracked daily before flowering and during the reproductive period. At the laboratory, 40 grains per panicle were separated by collecting 10 grains from each of four visually determined sections of the head. Fresh weight of the grains was first obtained, and then dry weight after drying those grains in an air-forced oven at 150°F until constant weight (Demarco et al., 2021). Grain weight, expressed as individual grain (mg), was calculated as the total grain dry weight divided to the total number of grains.

Grain filling rate and grain filling duration were estimated by fitting a bi-linear model [equations (1) and (2)] in each hybrid and source-sink treatment combination, with grain dry weight modeled on a day-time basis from flowering to harvest maturity:

$$\begin{aligned} \text{Grain weight (mg grain}^{-1}\text{)} &= a + b \times x && \text{for } x < c && [1] \\ \text{Grain weight (mg grain}^{-1}\text{)} &= a + b \times c && \text{for } x > c && [2] \end{aligned}$$

where x are the days after flowering, a is the y-intercept (mg grain⁻¹), b is the grain growth rate (mg grain/day), and c is the total duration of grain filling period (in days).

Mixed-effects models were fitted with the nlme (Pinheiro et al., 2018) package in RStudio (RStudio team, 2016) for each of the treatments done. The effect on all variables under study was determined through analyses of variance (ANOVA). Relationships among variables were described through linear regression analysis.

Results

Final weight was significantly affected by modifications of the source-sink ratio during grain filling ($P \leq 0.001$, Table 1). The average weight per kernel increased by 34 mg when treatment 2 was applied. In contrast, grain weight was drastically reduced to 21 mg when treatment 3 was applied. Grain weight remained relatively stable across different years of release, with no significant changes. The impact of source-sink treatments remained the same across different years of release (Figure 1A).

On the other hand, a significant increase in both yield and grain number has been observed with the year of release ($P \leq 0.1$ and $P \leq 0.01$, respectively; Figure 1B and 1C). In addition, both variables (yield and grain number) were negatively affected when source-sink manipulation treatments were applied. Grain number across all hybrids was reduced significantly up to 1526 grains per ft^2 when panicles were halved. Regarding yield, a decrease was recorded from 137 bu/a in the control to 104 bu/a when reducing the source, and 98 bu/a when reducing the sink ($P \leq 0.001$). These reductions in yield and grain number didn't show differences across different hybrids tested.

Furthermore, when analyzing grain filling dynamics, a bi-linear relationship within these two variables showed that variations in grain filling duration were responsible for the major changes in grain. The results showed that the grain filling rate ranged from 0.59 to 1.35 mg of grain/day and it was neither affected by the year of release nor source-sink manipulation. However, grain filling duration was significantly reduced, from an average of 31 days in the control treatment to 26 days in treatment 3 ($P \leq 0.05$, Figure 1D). Furthermore, this reduction was more noticeable in newer released hybrids achieving the shortest grain filling duration when the source was manipulated (19 days shorter in the newest hybrid) ($P \leq 0.05$).

In conclusion, there was no decrease in grain number when the defoliation was applied relative to the control across all hybrids. This result emphasizes that the application of defoliation (10 days after flowering) did not impact grain number set or increase abortion rates. In contrast, both yield and grain weight component were affected by defoliation. These results indicated that sorghum is mostly limited by source, in agreement with the outcomes presented by Gambin and Borrás (2007). An increase in yield due to genetic progress was also notable, with no differences in grain weight. Regarding grain filling period and dynamics, the defoliation effect was different throughout the years of release, where modern hybrids presented shorter duration of this stage. This reduction in the duration of the grain filling could be explained by a severe limitation on assimilates by defoliation, yet further analysis should be done to corroborate this hypothesis.

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Table 1. Analysis of variance and means for grain weight, grain number, yield, grain filling rate and duration for different years of release (YR) and three source-sink treatments (SS) in the 2021 field experiment

Year of release	Source-sink	Days to FL	Grain weight	Grain number	Yield	Grain filling rate	Grain filling duration
			mg/grain	ft ²	bu/a	mg grain/day	days
1960	Control	59	26.48	2909	132.1	1.03	31
1982	Control	61	25.63	2794	122.8	0.80	35
1997	Control	60	28.38	2629	128.0	1.15	30
2006	Control	59	28.23	2941	142.4	1.24	28
2010	Control	61	27.95	3350	160.6	1.22	29
2020	Control	60	30.29	2571	133.5	0.86	37
1960	Defoliation	58	21.47	2732	100.6	0.59	37
1982	Defoliation	61	20.55	2637	92.9	1.10	39
1997	Defoliation	61	19.91	3228	110.2	0.65	31
2006	Defoliation	59	19.69	3280	110.7	0.94	28
2010	Defoliation	61	22.31	2768	105.9	0.87	29
2020	Defoliation	61	20.32	3014	105.0	1.13	18
1960	Panicle halving	59	30.29	1585	82.3	1.22	30
1982	Panicle halving	61	36.47	1472	92.0	1.27	28
1997	Panicle halving	61	34.53	1885	111.6	1.18	30
2006	Panicle halving	58	35.42	1544	93.8	1.16	32
2010	Panicle halving	60	37.26	1448	92.5	1.10	31
2020	Panicle halving	58	32.19	2091	115.4	1.35	27
Source of variation							
Year of release (YR)			Ns	+	**	Ns	Ns
Source-sink (SS)			***	***	***	Ns	*
YR × SS			Ns	Ns	Ns	Ns	*

+ Significant at $P \leq 0.1$; * significant at $P \leq 0.05$; ** significant at $P \leq 0.01$; *** significant at $P \leq 0.001$. Ns: non-significant.

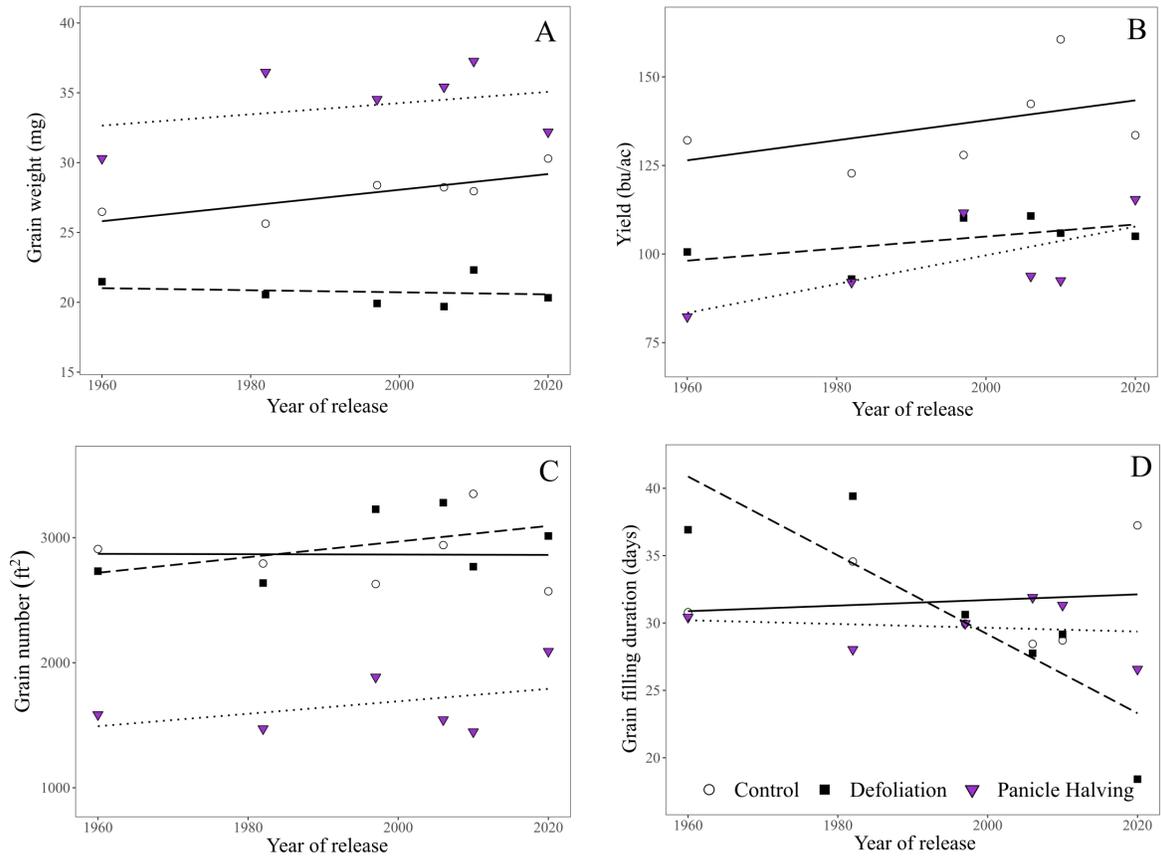


Figure 1. Grain weight (A), yield (B), grain number (C), and grain filling duration (D) across year of release (from 1960 to 2020). Source sink treatments: control = solid line and circles; defoliation = dashed line and squares; panicle having = dotted line and triangles.