

Plasticity of sorghum kernel weight to increased assimilate availability

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Abstract

Understanding source or sink limitations on crop yield is critical for the rational design of agricultural practices as well as breeding strategies. In the present article, we studied sorghum [*Sorghum bicolor* (L.) Moench] source–sink yield limitations during grain filling, and tested the hypothesis that the time in which kernel maximum water content is reached during grain filling defines a temporal limit for the crop to profit from source increases. Earlier studies have never tested increasing assimilate availability per kernel in different developmental stages. We conducted a field experiment increasing assimilate availability per kernel at anthesis and 15 days after anthesis in commercial hybrids. The anthesis treatment was aimed to increase assimilates per kernel from early grain filling, and the 15 days after anthesis treatment from the stage kernel maximum water content was achieved. Both treatments removed 50% of the kernels from one side of the panicle. Kernel dry weight (KW), kernel water content and kernel volume were measured in apical and basal positions of the panicle throughout grain filling. Increased assimilate availability always yielded a higher KW (~34% increase). This KW increase was consistent across the two kernel developmental stages when the treatment was imposed, the panicle position and hybrid. Achieving maximum water content did not prevent kernels from increasing their weight when assimilates were subsequently increased. Final KW was closely related to maximum kernel volume ($r^2 = 0.72$; $n = 42$; $p < 0.0001$). Increased assimilate availability per kernel promoted changes in both kernel growth rate and duration of grain filling.

We applied a quantitative approach for determining the magnitude of sorghum KW changes in response to assimilate availability changes during grain filling. This allowed us to compare our data to previously published articles, and to determine any general response pattern across environments. The analysis supported our observation that sorghum KW is highly responsive to increased assimilates, and indicated that increased assimilate availability during filling always increased sorghum KW. As such, growth of sorghum kernels is predominately source limited; breeding and management practices aimed to increase assimilate availability per kernel will be likely to enhance sorghum yield. Results show that the crop has the capacity to profit from source increases even after the initial grain-filling stages have occurred.

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1. Introduction

Understanding source or sink limitations on crop yield is critical for the rational design of agricultural practices as well as breeding strategies. Yield limitations due to the source or the sink capacity vary during the crop cycle. In the most important extensive crops yield is generally source limited during the

kernel set (Early et al., 1967; Pepper and Prine, 1972; Fischer, 1975). However, crop species differ in their relative source–sink yield limitation during the grain-filling period (Borrás et al., 2004). There has been some speculation about physiological processes responsible for differences among species (Kiniry et al., 1992; Andrade and Ferreiro, 1996; Egli, 1999; Borrás et al., 2004). In the present article, we studied sorghum source–sink yield limitations during grain filling, and tested the hypothesis that the time in which kernel maximum water content is reached during grain filling defines a temporal limit for the crop to profit from source increases (Borrás et al., 2004).

As seed density at physiological maturity is a rather stable trait, differences in seed dry weight among genotypes from the

Abbreviation: KW, kernel weight

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same species are usually related to variation in maximum seed volume. In cereals, maximum seed volume is established earlier than maximum dry weight, and is generally estimated as the developmental stage when kernel maximum water content is achieved (Saini and Westgate, 2000). Once maximum kernel volume is reached, biomass deposition replaces water within the kernel causing a progressive desiccation. Biomass accumulation ceases when a critical percent moisture content (water content per unit fresh weight) is reached (Egli and TeKrony, 1997; Saini and Westgate, 2000). As such, the time at which maximum water content is achieved appears to establish a temporal limit for the potential kernel sink capacity to be modified by the source activity (Borrás et al., 2004). Source increases later in development should have no impact in final kernel size because sink capacity is already established. As such, sink size would be the main limitation late in grain filling.

In sorghum, final KW is not limited by the maximum water content attained at mid grain filling (Gambín and Borrás, 2005). Kernels from apical and basal positions within the panicle reached maximum water content simultaneously, but differed in the timing when maximum kernel volume was attained. While apical kernels reached the maximum water content and volume at the same stage, basal kernels continued to expand and increase their volume until physiological maturity. These differences were related to changes in the rate water was lost from the kernels after maximum water content, apical kernels desiccated more quickly compared to basal ones (Gambín and Borrás, 2005). Desiccation is accelerated and the grain-filling period is reduced by source reduction during late grain development such as those caused by drought (Barlow et al., 1980; Brooks et al., 1982; Westgate, 1994), severe pathogen infestations (Pepler et al., 2006), or defoliations (Egharevba et al., 1976). This accelerated development limited the achievement of the earlier established kernel sink potential. Based on this evidence, we hypothesized that the normal accelerated desiccation rate from apical kernels of the panicle was source-related, and that the sink potential established at maximum water content in apical kernels is rarely achieved. If this is so, sorghum kernels could be defined as “plastic”, since they would be able to respond to source increases during the entire grain filling.

Past research altering the post-flowering source–sink ratio in sorghum has shown that KW significantly changes due to increases or decreases in assimilate availability during grain filling (Fischer and Wilson, 1975a,b; Muchow and Wilson, 1976; Hamilton et al., 1982; Heiniger et al., 1993a). However, manipulative treatments testing how kernels respond to an increased assimilate availability have always been imposed no later than 7 days after anthesis (Fischer and Wilson, 1975a,b; Heiniger et al., 1993a). This did not allow the testing of source or sink limitations late in grain filling. Also, although these articles confirm that sorghum KW (and yield) can be source limited to some degree, they did not quantify the magnitude of source limitation. To estimate this magnitude across genotypes, environments and manipulative treatments, we applied a quantitative approach to compare KW response to assimilate availability changes in published studies (Slafer and Savin, 1994; Borrás et al., 2004).

We studied how sorghum KW is affected when the source–sink ratio during grain filling is increased at two stages of grain filling: anthesis and at 15 days after anthesis. The first treatment was aimed at increasing assimilate availability per kernel at the start of grain filling, and the second from the time at which maximum water content was achieved. Kernel development was examined in a range of hybrids differing in kernel size, and quantitatively analyzed together with published results. We describe how kernel water relations change in response to varying assimilate availability conditions during grain filling. These results help explain the developmental plasticity of sorghum kernels in relation to assimilate availability and its impact on yield formation.

2. Materials and methods

2.1. Field experiment and measurements

The field experiment was conducted at the Department of Plant Production, University of Buenos Aires (35°35'S, 59°29'W), on a silty clay loam soil (Vertic Argiudol). Details of this experiment have been previously described in Gambín and Borrás (2005). Seven current Argentine commercial hybrids (DA48, DK51, DK68T, X7761, DK61T, DK39T and X9946) from Monsanto Argentina differing in final KW and tannin content (Monsanto Argentina, 2003; Vicente Trucillo, personal communication) were sown on 12 October 2002. Treatments were arranged in a randomized complete block design with three replicates. Each replicate consisted of five rows 0.5 m apart and 4 m long. Plots were over-sown and thinned after emergence to a final stand density of 200,000 plants ha⁻¹. Plots were irrigated to complement the natural rainfall throughout the crop cycle and to avoid water stress. Fertilizer was applied twice: before sowing (70 kg N ha⁻¹) and post-emergence (100 kg N ha⁻¹) between the fourth- and six-leaf stages (ligulated leaves). Weeds and tillers were manually removed periodically throughout the growing cycle.

Sorghum panicles have a basipetal anthesis pattern (Doggett, 1970; Heiniger et al., 1993b). Anthesis of basal flowers occurs 4–10 days after the apical section; anthesis dates were recorded for apical and basal sections after dividing the panicle into four equal sections on the basis of the number of whorls on the rachis (Heiniger et al., 1993a). Anthesis was considered when at least one anther was exposed from any panicle section. In this experiment, anthesis of the basal part of the panicle was 2–4 days after apical anthesis in all hybrids (Gambín and Borrás, 2005). Treatments were imposed at anthesis and 15 days after anthesis of the apical florets. Both treatments consisted in completely removing all the branches from one side of the panicle with a scissors. The goal was to remove 50% of the kernels with a uniform distribution across the four panicle positions (Heiniger et al., 1993a). To do so, the number of branches per whorl were counted and half of them removed. At physiological maturity, the number of kernels per panicle was determined by counting a minimum of three plants per replicate from all treatments.

The first treatment was aimed to increase assimilate availability per kernel during the entire grain-filling period,

and the second from the stage kernel maximum water content is achieved. The timing of the later treatment was based on how kernel water content develops in wheat (*Triticum aestivum*) and maize (*Zea mays* L.), since the maximum value is normally attained during mid grain filling (Martinez-Carrasco and Thorne, 1979; Westgate, 1994). Beginning at apical floret anthesis, one panicle per replicate was harvested every 3–5 days. Twenty-five kernels from positions 1 and 4 (Heiniger et al., 1993a,b) were sampled for fresh and dry weight as previously described (Gambín and Borrás, 2005).

Kernel dry weight was determined after drying the kernels in a forced air oven at 70 °C for at least 96 h. These data were used to calculate kernel water content (mg kernel^{-1}) and percent kernel moisture (g kg^{-1}) during grain filling. Starting fifteen days after floret apical anthesis, 10–15 kernels taken from each position of the same harvested panicle were used to determine kernel volume by volumetric displacement (Martinez-Carrasco and Thorne, 1979; Kiniry, 1988).

Final KW, kernel growth rate during the effective grain-filling period and total duration of grain filling for each hybrid, position and source–sink ratio treatment were determined by fitting a trilinear model (Eqs. (1)–(3)):

$$\text{KW} = a + b \text{ TT}, \quad \text{for } \text{TT} < = c \quad (1)$$

$$\text{KW} = a + bc + d(\text{TT} - c), \quad \text{for } \text{TT} > c \text{ and } \text{TT} < e \quad (2)$$

$$\text{KW} = a + bc + d(e - c), \quad \text{for } \text{TT} > = e \quad (3)$$

where KW is kernel weight, TT thermal time after anthesis, a the Y -intercept (mg), b the kernel growth rate during the lag phase ($\text{mg } ^\circ\text{C day}^{-1}$), c the duration of the lag phase ($^\circ\text{C day}$), d the kernel growth rate during the effective grain-filling period ($\text{mg } ^\circ\text{C day}^{-1}$) and e is the total duration of grain filling ($^\circ\text{C day}$). The trilinear model was fitted to the kernel dry weight data using the iterative optimization technique in Table Curve V 3.0 (Jandel Scientific, 1991). The adjusted r^2 values always ranged from 0.96 to 0.99. Daily thermal time values were obtained using a base temperature of 5.7 °C (Heiniger et al., 1993a). Mean daily air temperature was calculated as the average of daily maximum and minimum air temperatures registered at a weather station 50 m from the experiment. The thermal time after anthesis for each sample was always referred to its own apical or basal anthesis date.

Percent moisture content values at physiological maturity were determined using a bilinear model relating kernel dry weight and kernel moisture content data (Eqs. (4) and (5)) (Jandel Scientific, 1991):

$$\text{KW} = f - g \text{ Mc}, \quad \text{for } \text{Mc} > = h \quad (4)$$

$$\text{KW} = f - gh, \quad \text{for } \text{Mc} < h \quad (5)$$

where KW is kernel weight, Mc the percent moisture content (in g kg^{-1}), f the Y -intercept (mg), g the rate of kernel moisture decline during grain filling [$\text{mg} (\text{g kg}^{-1})^{-1}$] and h is the critical percent moisture content at physiological maturity (g kg^{-1}). The adjusted r^2 values ranged from 0.93 to 0.99.

Maximum water content and maximum kernel volume were determined as the maximum value registered in each hybrid \times treatment \times panicle position replicate plot. Kernel volume increases after the achievement of the maximum water content were calculated as the difference between kernel volume attained at physiological maturity and the kernel volume at maximum water content measured in each hybrid \times treatment \times panicle position combination. Differences among hybrids, source–sink ratio treatments and panicle positions were determined by ANOVA as a split plot design, with hybrids as main plots, source–sink ratio treatments as sub-plots and panicle positions as sub-sub-plots.

2.2. Literature review

Data from previous studies that described sorghum KW response to assimilate availability changes during grain filling were analyzed using a quantitative approach. For each study, modifications in the potential availability of assimilates per growing kernel produced during grain filling were evaluated in relation to the untreated control; the same was done for kernel dry weight. For example, a 50% kernel removal treatment at flowering that increased kernel size from 30 to 33 mg kernel^{-1} was assumed to be a 100% increase in potential assimilate availability per kernel that resulted in a 10% increase in kernel dry weight when both variables are compared with the untreated control. When the assimilate availability manipulations were imposed during mid grain filling, we estimated the potential assimilate availability change by taking into account the proportion of the grain-filling period affected. That is, a treatment removing 50% of the kernels when 40% of the grain-filling period had already elapsed would be represented as a 60% increase in potential assimilate availability per kernel in relation to the untreated control. Other examples of the methodology are described in Slafer and Savin (1994) and Borrás et al. (2004).

The main assumption of the methodology is that the sink strength has no effect on the non-manipulated source capacity (Borrás et al., 2004). We are aware of evidence showing re-adjustments in canopy photosynthesis to compensate for artificially imposed alterations in the source–sink ratio during grain filling. This response, however, has always been minor when compared with the magnitude of the source–sink manipulation. So, in some cases the increases in assimilate availability per seed due to sink removal may have been slightly over estimated if the treatment resulted in a reduction in canopy photosynthesis. A second assumption was made in relation to the source provided by organs other than green leaves in sorghum. We assumed that the panicle intercepted 18% of the solar radiation (Fischer and Wilson, 1971), so an additional correction was made to data obtained from defoliation experiments.

To describe responses of kernel dry weight (Y) relative to the change in potential assimilate availability per kernel (X) across all genotypes and environments, we fitted a bilinear model with a plateau (Eqs. (6) and (7)):

$$Y = i + jX, \quad \text{for } X \leq k \quad (6)$$

Table 1

Kernel number per panicle, mean kernel weight, yield per panicle and final kernel weight in kernels from apical (A) and basal (B) positions within the panicle for the seven hybrids tested under the different source–sink ratio treatments. The anthesis treatment consisted in removing an entire side of the panicle at apical anthesis. The 15 days after anthesis treatment was similar but performed 15 days after apical anthesis

Hybrid	Treatment	Kernel number per panicle	Mean kernel weight per panicle ^a (mg kernel ⁻¹)	Yield per panicle (g panicle ⁻¹)	Panicle position	Kernel weight (mg kernel ⁻¹)
DA48	Control	3067	20.9	64.2	A	21.3
					B	21.8
	Anthesis	1570	28.0	43.8	A	25.5
					B	29.3
	15 days after anthesis	1405	27.6	38.8	A	24.8
					B	28.3
DK51	Control	2686	19.1	51.2	A	19.9
					B	20.4
	Anthesis	1247	27.4	33.7	A	29.2
					B	27.0
	15 days after anthesis	1547	28.0	43.2	A	27.4
					B	28.0
DK68T	Control	2474	21.7	53.8	A	22.3
					B	21.6
	Anthesis	1222	30.1	36.7	A	27.7
					B	29.1
	15 days after anthesis	1219	29.9	36.6	A	27.3
					B	30.1
X7761	Control	3486	21.7	75.5	A	23.5
					B	25.1
	Anthesis	1394	33.3	46.2	A	33.1
					B	34.0
	15 days after anthesis	1317	32.7	43.0	A	30.5
					B	29.6
DK61T	Control	3537	17.6	62.0	A	16.5
					B	17.8
	Anthesis	1529	25.9	39.3	A	24.5
					B	24.3
	15 days after anthesis	1684	28.0	47.1	A	23.8
					B	27.8
DK39T	Control	2539	21.3	54.2	A	21.8
					B	21.9
	Anthesis	1350	27.8	37.4	A	26.4
					B	28.6
	15 days after anthesis	1247	27.4	34.2	A	25.7
					B	28.5
X9946	Control	3147	20.1	63.3	A	18.5
					B	20.0
	Anthesis	1508	28.2	42.4	A	26.1
					B	27.7
	15 days after anthesis	1310	27.8	36.3	A	26.7
					B	27.3
Mean	Control	2991	20.3	61.0	A	20.5
					B	21.2
	Anthesis	1403	29.0	40.0	A	27.5
					B	28.6
	15 days after anthesis	1390	29.0	40.0	A	26.6
					B	28.5
Hybrid (H)		(306) ^{*†}	(1.7) ^{***}	(7.5) [*]		***
Treatment (T)		(180) ^{***}	(0.87) ^{***}	(4.3) ^{***}		***
H × T		NS (477)	NS (2.3)	NS (11.4)		*
Position (P)						***
H × P						**
T × P						**
H × T × P						(1.6) ^{**}

***, ***, ** Significant at $P = 0.05$, 0.01 and 0.001 , respectively; NS: not significant. [†]LSD value for $P \leq 0.05$.

^a Mean kernel weight was obtained dividing yield per panicle by the kernel number per panicle.

$$Y = l, \quad \text{for } X > k \quad (7)$$

where i is the intercept, j the slope at the response part of the curve, k the saturation value at which further increases in relative assimilate availability per kernel are no longer expected to increase relative kernel dry weight, and l is the plateau value that summarizes the maximum kernel dry weight as a percentage of the controls. The model was fitted using an iterative optimization technique (Jandel Scientific, 1991). This bilinear model was used as a simplification of the theoretical hyperbolic model (Jenner et al., 1991). It simply predicts there is a response range where any change in assimilate availability impacts kernel dry weight. And from a particular threshold upwards, kernels grow in a saturation medium that maximizes kernel dry weight.

3. Results and discussion

3.1. Sorghum kernel weight response to source–sink manipulations

Hybrids differed in the number of kernels per plant ($p < 0.05$), mean KW ($p < 0.001$) and final yield ($p < 0.05$; Table 1). Kernel removal treatments effectively reduced kernel number per panicle to 50% relative to the untreated control ($p < 0.001$). Treatments imposed at anthesis and 15 days later significantly increased mean KW ($p < 0.001$) to a similar extent relative to the control. Reduced kernel number per plant at both stages decreased yield per panicle ($p < 0.001$) with no difference between treatments. There was no significant hybrid \times treatment interaction across these traits, showing all hybrids responded similarly to the source–sink manipulation (Table 1).

The pattern of kernel dry weight accumulation was significantly affected by the source–sink manipulations in all hybrids and panicle positions (Fig. 1). There was a three-way interaction between hybrid, treatment, and panicle position for final KW ($p < 0.01$; Table 1). This result indicates that increases in KW depended upon the hybrid, the stage of development when the source per kernel was increased, and the floret position within the panicle. Nonetheless, it was clear that the large increase in mean KW for the panicle in response to increased assimilate availability per kernel reflected an increase in KW at both apical and basal floret positions in all hybrids ($p < 0.01$; Table 1; Fig. 1). Averaged across hybrids, the relative change in final KW was about 34% for apical and 35% for basal kernels when the source per kernel was increased at anthesis. The increase was about 30% for apical and 34% for basal kernels for the 15 days after anthesis treatment. As such, increasing assimilate availability at anthesis or 15 days later increased both apical and basal KW to nearly the same extent. This result illustrates the high plasticity of developing sorghum kernels to alter their weight in response to increased assimilate availability starting from different grain-filling stages. The response to our treatment 15 days after anthesis showed that the crop has the capacity to profit from source increases even after the initial grain-filling stages have occurred.

A quantitative approach was used to pool our results with previously published KW responses to altered source–sink ratios after flowering. Table 2 lists the published articles included in this analysis. As shown in Fig. 2A, these studies revealed sorghum KW to be highly responsive to increased availability of assimilates per kernel. Mean KW response to increased assimilates was about 44% relative to the untreated control. This mean KW response to increases in assimilate availability per kernel was attained at ca. 104% relative change in assimilate availability per kernel. Most interestingly, there was no case in which increased assimilate availability did not increase final sorghum KW (no data points over the 1:0 line). It was clear that our data matched the response pattern shown by previously reported studies (Fig. 2B). These results confirm our observation that growth of sorghum kernels is generally source limited, and final KW is generally well below the potential weight. This situation is different to wheat and maize, and similar to soybean (*Glycine max* L.) (Borrás et al., 2004), but soybean shows greater variation between genotypes and environments.

Analysis of the literature values also showed that sorghum KW was reduced significantly when source per kernel was decreased during grain filling, although a large variation in response was apparent (Fig. 2). The mean slope between changes in KW and reductions in assimilate availability per kernel during grain filling was 0.39. This illustrates that sorghum kernel growth depends on the amount of current assimilates produced during grain filling, and that stored assimilates can also be important to support kernel growth.

3.2. Kernel water relations and kernel sink plasticity

These results showed the high plasticity of sorghum kernels to increase their weight when assimilate availability per kernel was increased across a wide range of genotypes and environments (Fig. 2). This drew our attention to try to understand the particular mechanisms behind this plasticity. We studied the sorghum kernel water relations for this purpose.

The patterns of kernel water content and volume development during grain filling were clearly affected by the source–sink manipulation treatments (Figs. 1 and 3). Increasing source per kernel at anthesis or 15 days later increased both maximum water content and maximum kernel volume ($p < 0.001$) in a similar way in all hybrids (Table 3). Only the increase in maximum water content showed a treatment \times panicle position interaction ($p < 0.001$). Averaged across hybrids, the relative change in maximum water content was about 17% for apical and 33% for basal kernels when the source per kernel was increased at anthesis. The change was about 5% for apical and 23% for basal kernels when the source was increased 15 days after anthesis. As such, the large increase in final KW (>30% averaged across hybrids) was not correlated with the same increase in maximum water content (Fig. 4A). The response of final KW was more closely related to changes in maximum kernel volume (Fig. 4B).

In the untreated control, there was no further increase in kernel volume of apical kernels after they reached maximum

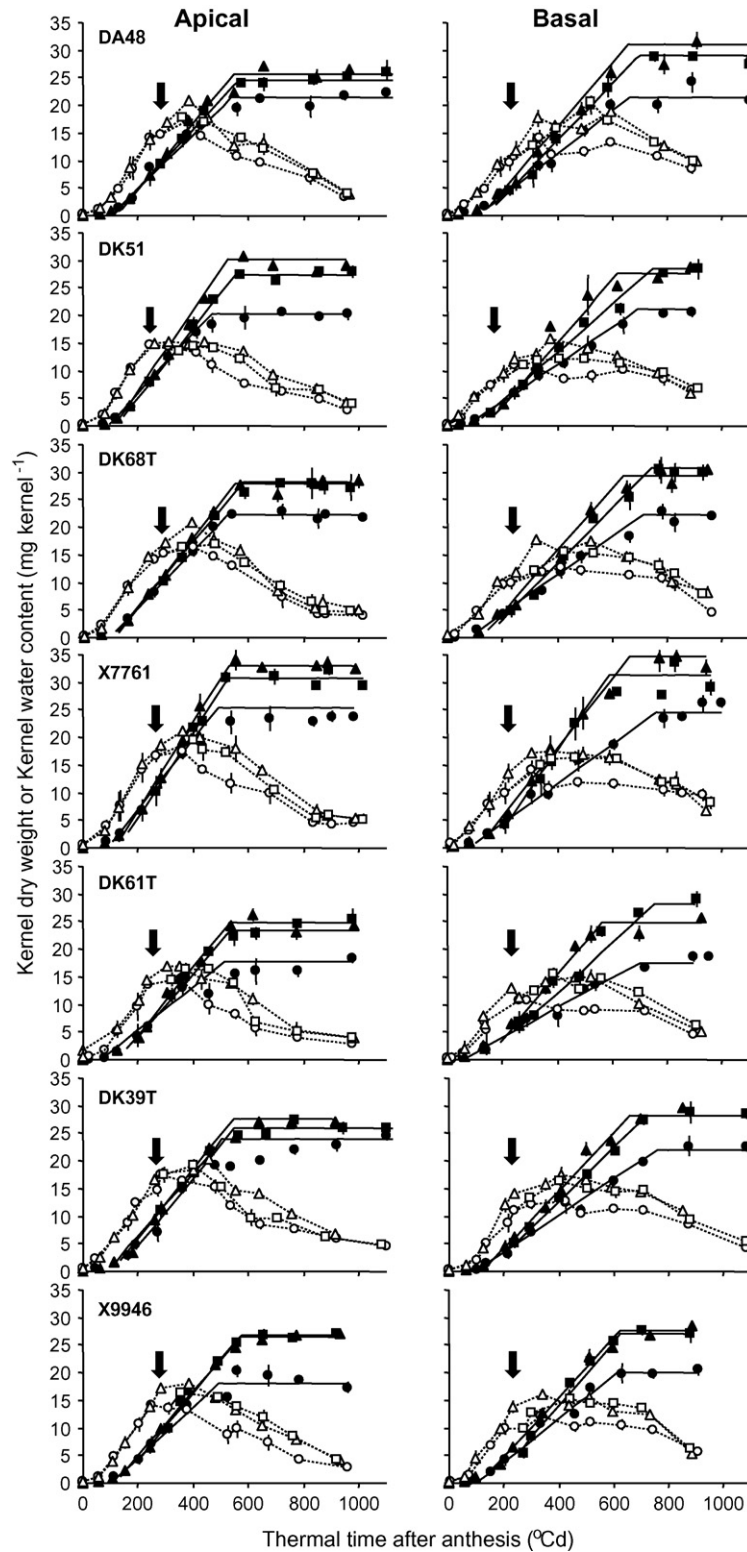


Fig. 1. Kernel dry weight (closed symbols, full lines) and kernel water content (open symbols, dotted lines) development during grain filling for apical and basal kernels in the seven sorghum hybrids. Accumulated thermal time after anthesis was calculated from the apical or basal panicle anthesis date of the particular hybrid. Treatments are represented as: circles, untreated control; triangles, increased source per kernel at apical anthesis; squares, increased source per kernel 15 days after apical anthesis. Both treatments removed 50% of the kernels. Arrows indicate the date when the post-anthesis treatment was performed in each hybrid and panicle position.

Table 2
Description of the number of tested genotypes, the type of manipulative treatment used to alter the assimilate availability per kernel during grain filling, and the country where the experiment was conducted

Number of genotypes	Type of treatment	Country	Authors
2	Chemical leaf desiccation	Israel	Blum et al. (1997)
1	Seed removal, stand reduction, shading	Australia	Fischer and Wilson (1975a)
1	Stand reduction	Australia	Fischer and Wilson (1975b)
1	Seed removal	India	Hamilton et al. (1982)
1	Defoliation, stand reduction, shading	USA	Heiniger et al. (1993a)
2	Shading	USA	Kiniry (1988)
2	Seed removal, stand reduction, shading	Australia	Muchow and Wilson (1976)
1	Defoliation	USA	Rajewski and Francis (1991)
1	Seed removal	Mexico	Valadez-Gutiérrez et al. (2006)
7	Seed removal	Argentina	Present article

water content (Fig. 5). The volume of apical kernels at physiological maturity was less than the maximum established at maximum water content (Fig. 5), suggesting that these kernels had a potential sink capacity that was not achieved. The volume of basal kernels, however, continued to increase late in grain filling (Fig. 5), after maximum water content. Enhancing

source per kernel at anthesis or 15 days after anthesis increased the volume of apical kernels after maximum water content was reached (Fig. 5). This continued increase in volume was similar to that observed in basal kernels on the untreated control panicles (Fig. 5). These findings illustrate the plasticity of sorghum kernels, as the achievement of maximum water content was not creating a sink limitation to increments in source availability. Apical kernels continued to expand and increased their final weight about 30% when increased assimilates were made available in the 15 days after anthesis treatment. Maximum water content, however, only increased about 5% (Fig. 4A). This potential for continued expansion contrasts with the response of maize and wheat, which have shown little or no KW response to increases in source availability during the effective grain-filling period (Fischer and HilleRisLambers, 1978; Andrade and Ferreiro, 1996; Borrás et al., 2004). Kernels from maize and wheat have shown water content developmental patterns during grain filling that were similar to sorghum, but KW has always been limited by the maximum water content attained earlier in development (Saini and Westgate, 2000; Borrás et al., 2003).

We previously showed a consistent relationship between kernel growth rate and maximum water content across hybrids and panicle positions (Gambín and Borrás, 2005). This relationship was maintained with results corresponding to source–sink ratio treatments altering the assimilate availability per growing kernel at different stages of grain filling ($r^2 = 0.53$; $p < 0.001$; $n = 42$). Kernel growth rate varied across hybrids ($p < 0.01$) and panicle positions ($p < 0.001$), and a hybrid \times position interaction ($p < 0.05$) was detected (Table 3). Enhancing the source–sink ratio greatly increased the kernel growth rate during the effective grain-filling period ($p < 0.001$); the increase varied with the kernel position within the panicle ($p < 0.05$). Apical kernels always had higher growth rates than basal kernels, and basal kernels increased their rate more than apical ones in response to increased assimilate availability (Table 3; Fig. 1). Similar results were reported by Heiniger et al. (1993a) when the source per kernel was increased by stand density reductions during the early stages of grain filling. In rice (*Oryza sativa* L.), which displays inflorescence and flowering dynamics similar to sorghum, the typically slow kernel growth of basal kernels could be increased

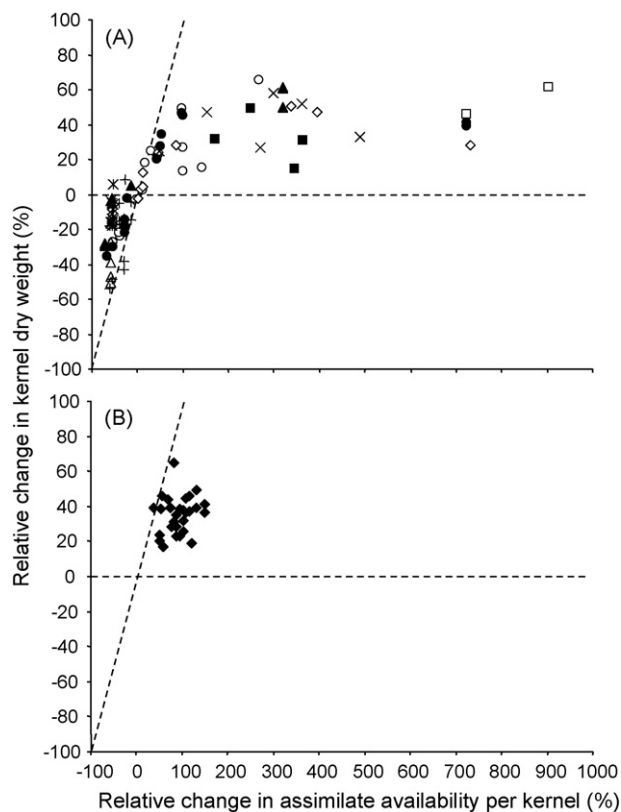


Fig. 2. Relationship between sorghum relative change in final kernel weight and the relative change in potential assimilate availability per kernel produced during grain filling in a number of previously published experiments (A), and for the one described in the present article (B). Dashed lines stand for the theoretical slopes of 1 (full source limitation) and 0 (full sink limitation). The total number of data points is 125. (●) Fischer and Wilson (1975a), (○) Muchow and Wilson (1976), (▲) Heiniger et al. (1993a), (△) Blum et al. (1997), (■) Kiniry (1988), (×) Valadez-Gutiérrez et al. (2006), (□) Fischer and Wilson (1975b), (◇) Hamilton et al. (1982), (X) Pepper and Prine (1972), (+) Rajewski and Francis (1991), and (◆) present article.

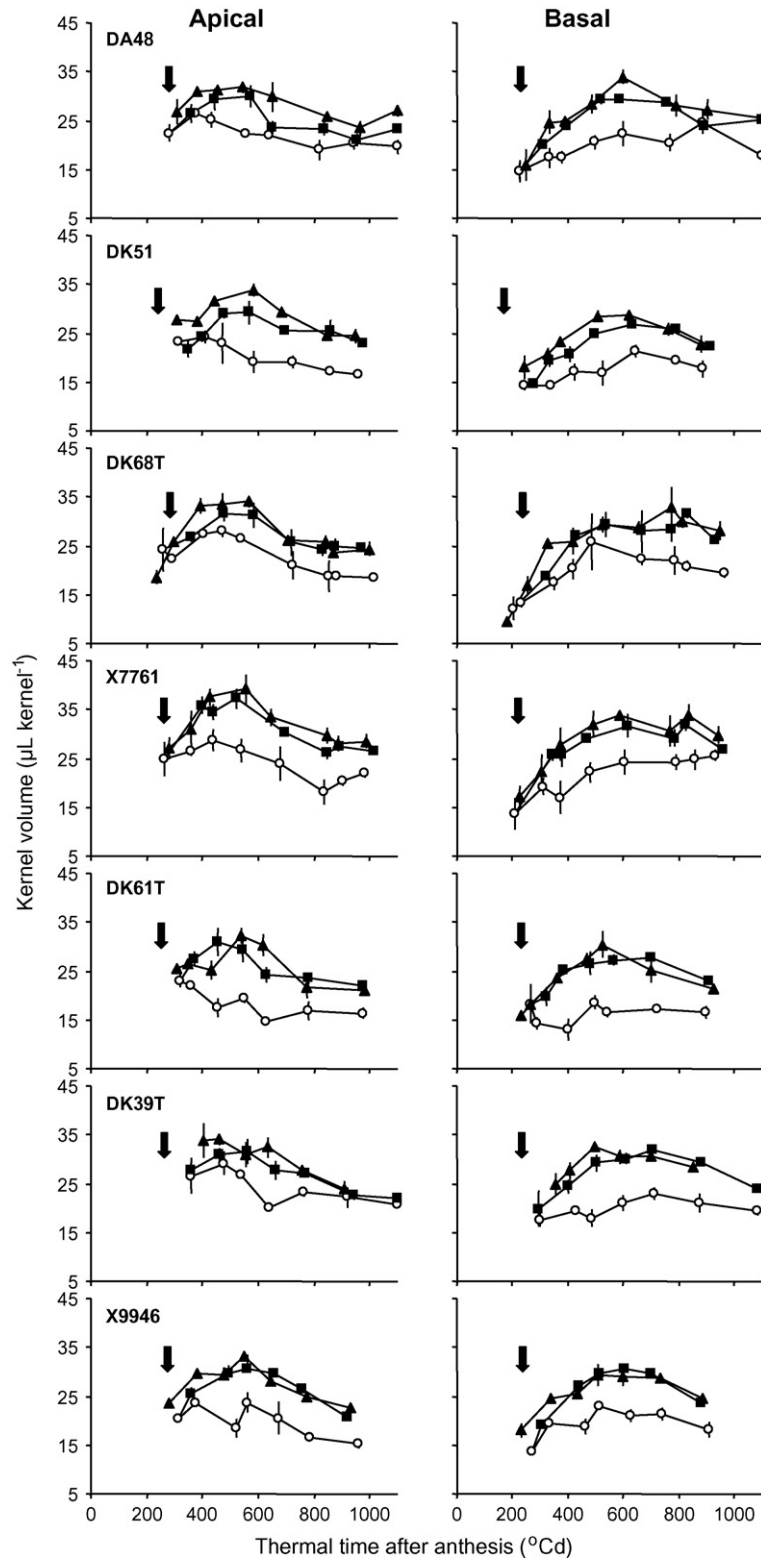


Fig. 3. Kernel volume development during grain filling for apical and basal kernels in seven sorghum hybrids. Treatments are represented as: circles, untreated control; triangles, increased source per kernel at apical anthesis; squares, increased source per kernel 15 days after apical anthesis. Both treatments removed 50% of the kernels. Arrows indicate the date when the post-anthesis treatment was performed in each hybrid and panicle position.

to achieve rates similar to the apical ones when source availability was increased at anthesis (Ishimaru et al., 2005).

When studying how kernels from different panicle positions develop, we previously noted apical kernels to have a shorter

duration of grain filling when compared to basal ones. We also reported that these differences were related to a higher rate of water loss after maximum water content was reached, which was reflected in a faster percent moisture content decline during

Table 3
Maximum water content, maximum kernel volume, kernel growth rate during the effective grain-filling period, total duration of grain filling and percent moisture content at physiological maturity (PM) in kernels from apical (A) and basal (B) positions within the panicle for the seven hybrids tested under different source–sink ratio treatments. The anthesis treatment consisted in removing an entire side of the panicle at apical anthesis. The 15 days after anthesis treatment was similar but performed 15 days after apical anthesis. Both treatments removed 50% of the kernels

Hybrid	Treatment	Panicle position	Maximum water content (mg kernel ⁻¹)	Maximum kernel volume (μL kernel ⁻¹)	Kernel growth rate (mg °C day ⁻¹ 10 ⁻²)	Total duration of grain filling (°C day)	Moisture content at PM (g kg ⁻¹)
DA48	Control	A	17.3	27.3	4.9	536	362
		B	14.9	28.0	3.9	665	316
	Anthesis	A	20.8	33.2	6.1	547	384
		B	19.2	33.9	5.8	660	291
	15 days after anthesis	A	17.7	31.7	5.4	569	356
		B	19.9	30.9	5.1	700	306
DK51	Control	A	14.8	26.3	5.4	465	372
		B	12.0	21.7	3.4	693	281
	Anthesis	A	15.5	34.4	7.3	526	300
		B	16.2	29.2	5.7	618	255
	15 days after anthesis	A	15.0	31.7	6.4	550	262
		B	12.4	27.5	4.3	750	216
DK68T	Control	A	16.5	30.1	5.3	523	380
		B	13.3	26.9	3.5	714	304
	Anthesis	A	20.9	36.1	6.4	554	357
		B	18.6	34.5	5.7	642	290
	15 days after anthesis	A	17.3	32.1	5.9	581	314
		B	16.0	33.5	5.1	742	280
X7761	Control	A	18.4	30.9	6.3	490	378
		B	14.8	28.5	4.0	761	241
	Anthesis	A	21.8	40.0	9.0	513	332
		B	18.0	37.6	6.3	661	279
	15 days after anthesis	A	18.9	37.5	7.8	528	333
		B	17.3	35.1	7.3	587	285
DK61T	Control	A	15.3	24.1	4.8	514	396
		B	11.1	22.2	2.7	701	292
	Anthesis	A	17.3	31.4	6.2	529	350
		B	15.6	33.4	5.9	561	311
	15 days after anthesis	A	17.1	32.9	5.8	534	327
		B	15.6	30.7	4.6	752	251
DK39T	Control	A	17.8	29.7	5.8	504	364
		B	13.8	25.5	3.3	761	278
	Anthesis	A	20.4	36.3	6.3	546	381
		B	18.3	32.9	5.2	546	286
	15 days after anthesis	A	19.1	33.4	6.2	657	369
		B	16.6	33.4	4.8	721	283
X9946	Control	A	15.2	24.8	4.7	493	338
		B	12.4	23.7	3.9	611	293
	Anthesis	A	18.0	30.3	5.8	574	321
		B	16.7	29.5	5.4	625	277
	15 days after anthesis	A	16.4	32.0	6.1	570	321
		B	15.4	31.2	5.8	625	310
Mean	Control	A	16.5	27.6	5.3	504	370
		B	13.2	25.2	3.5	701	286
	Anthesis	A	19.2	34.5	6.7	541	346
		B	17.5	33.0	5.7	616	284
	15 days after anthesis	A	17.4	33.0	6.2	570	326
		B	16.2	31.8	5.3	697	276
Hybrid (H)		(1)***	(2)***	(0.6)**	NS	**	
Treatment (T)		***	***	***	*	***	
H × T		NS	NS	NS	NS	(29)**	
Position (P)		***	(0.9)***	***	***	***	
H × P		NS	NS	(0.7)*	NS	NS	
T × P		(0.7)***	NS	(0.4)*	(37)***	(18)*	
H × T × P		NS	NS	NS	NS	NS	

***, ***, * Significant at $P = 0.05$, 0.01 and 0.001 , respectively; NS: not significant. †LSD value for $P \leq 0.05$.

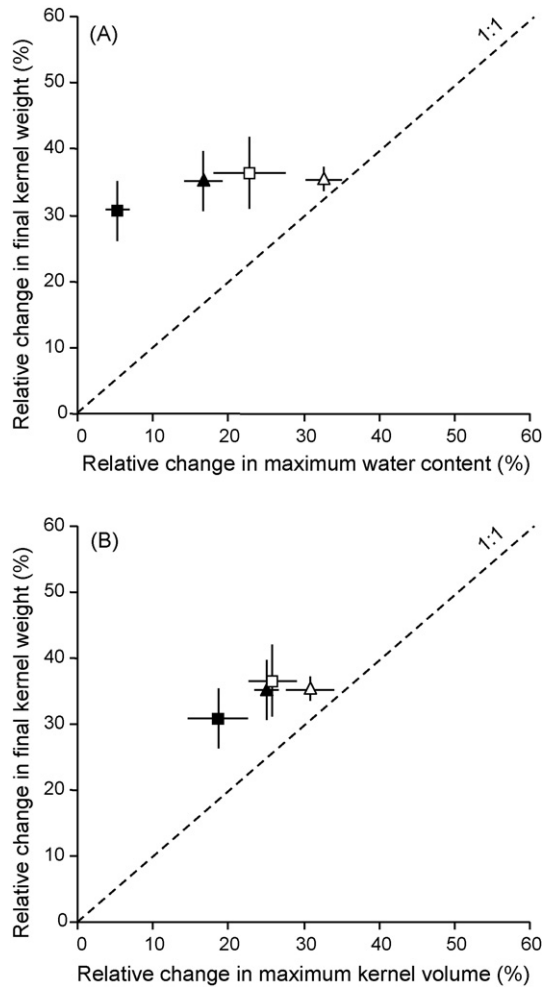


Fig. 4. Relation between the relative change in final kernel weight and the relative change in maximum water content (A), and between the relative change in final kernel weight and the relative change in maximum kernel volume (B) from the increased assimilate availability treatments, in kernels from apical (closed symbols) and basal (open symbols) positions within the panicle. Values are relative to the untreated control for each particular hybrid \times panicle position combination. For clarity, they represent the mean of seven hybrids, and bars indicate the S.E. Treatments are represented as: triangles, increased source per kernel at anthesis; squares, increased source per kernel 15 days after anthesis. Both treatments removed 50% of the kernels.

late grain filling (Gambín and Borrás, 2005). Apical kernels also ceased the deposition of biomass at higher percent moisture content values. Enhanced source per kernel increased the grain-filling duration of the apical kernels and was independent of the stage this increase started ($p < 0.001$; Table 3). Yet, for basal kernels, enhancing source per kernel at anthesis shortened the duration of grain filling, but had no effect when the treatment was imposed 15 days later (Table 3; Fig. 1). These changes in duration of grain filling promoted by source–sink manipulations were consistent with changes in the kernel water relations. At increased source conditions, apical kernels lost water more slowly after maximum water content, similarly to the basal ones (Fig. 6). In addition, enhancing source per kernel always reduced the percent moisture content at physiological maturity in apical kernels; there were no apparent changes in kernel percent moisture at physiological maturity in

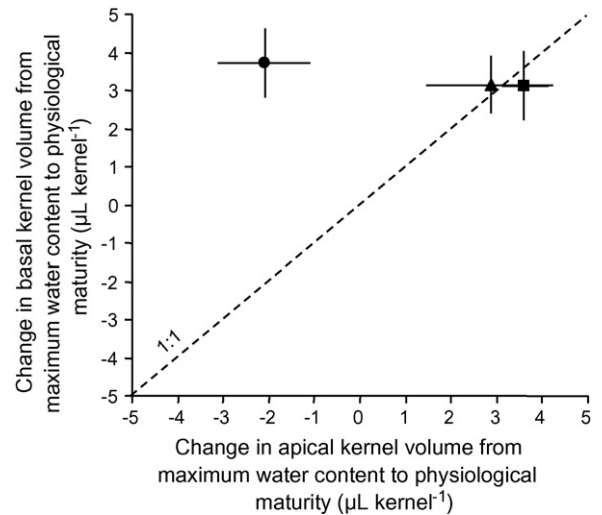


Fig. 5. Relation between changes in kernel volume from maximum water content to physiological maturity in kernels from apical and basal positions within the panicle. Values represent the mean of seven hybrids, and bars represent the S.E. Treatments are represented as: circles, untreated control; triangles, increased source per kernel at anthesis; squares, increased source per kernel 15 days after anthesis. Both treatments removed 50% of the kernels.

basal ones ($p < 0.05$; Table 3). There was a general negative correlation between the duration of grain and the percent moisture content at physiological maturity ($r^2 = 0.60$; $p < 0.001$; $n = 42$).

Variations in the critical percent moisture content at physiological maturity within a species are known to be smaller than those among species (Egli and TeKrony, 1997; Saini and Westgate, 2000). However, we found differences in this critical value not only between panicle positions but also among hybrids ($p < 0.01$; Table 3). In addition, a hybrid \times treatment interaction showed that not all hybrids responded similarly to the increase in assimilate availability ($p < 0.01$; Table 3). Further studies are needed to clarify what process might be behind these changes. An early evidence in maize has already showed that extreme source–sink manipulations may impact the critical percent moisture content at which biomass deposition stops (Afuakwa et al., 1984).

In other species like soybean, the duration of grain filling has been related to the time in which maximum water content is attained (Egli, 1990); the later in development the maximum content is achieved, the longer the seed maintains a water status favorable for continued storage product deposition. Under conditions of enhanced assimilate availability, sorghum kernels always achieved maximum water content later in development ($p < 0.05$), with no differences between panicle positions or hybrids (Fig. 6). However, because increasing assimilates per kernel would decrease or increase the duration of grain filling depending on the panicle position, there was no clear relationship between the grain-filling duration and the time in which maximum water content was achieved ($p < 0.83$).

Panicle positions and treatments showed a big range in the amount of biomass accumulated from maximum water content to physiological maturity for a similar amount of water lost from the kernels during the same period (Fig. 7). This was

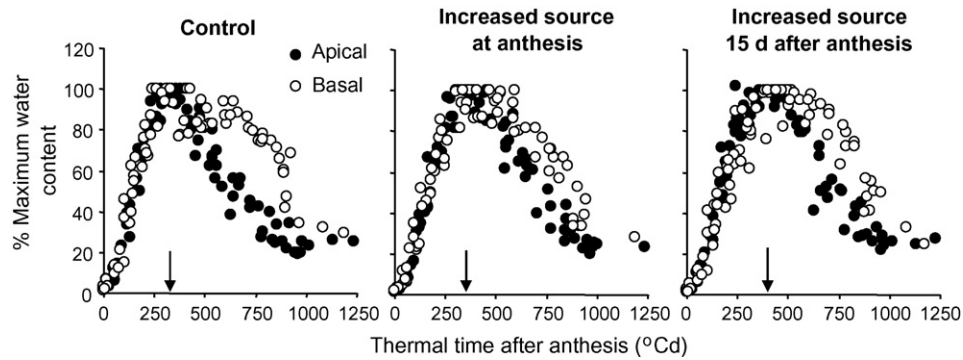


Fig. 6. Evolution of kernel water content during grain filling shown as a percentage of the maximum value in kernels from apical (closed symbols) and basal (open symbols) positions within the panicle for the untreated control, increased source per kernel at anthesis, and increased source per kernel 15 days after anthesis. Arrows indicate the moment maximum water content was reached within each source treatment (316, 364 and 410 °C day for control, anthesis and 15 days after anthesis, respectively); no differences in timing were detected between hybrids ($p > 0.05$) or positions ($p > 0.05$) within each source treatment. Both treatments removed 50% of the kernels.

important to understand the particular plasticity this species has to assimilate availability changes during grain filling. Differences in the percent moisture content at physiological maturity, and in the pattern of water development after maximum water content were the processes behind this variability, allowing kernels to expand and accumulate different amounts of biomass during late grain filling.

As in other seeds, sorghum kernel density increases throughout grain filling (Gambín and Borrás, 2005). Source–sink ratio treatments had no effect on the pattern of kernel density increase when plotted on a kernel percent moisture content basis (Fig. 8).

Together, these results support the conclusion that contrasting growth patterns between apical and basal panicle positions are partially source-related. Differences in kernel growth

became smaller when source per kernel increased. Differences in kernel growth between positions within reproductive structures in crops other than sorghum are usually explained by differences in the potential sink size defined early in grain filling (Brocklehurst, 1977; Tollenaar and Daynard, 1978; Reddy and Daynard, 1983; Lindström et al., 2006). In sorghum, however, differences in kernel growth within the sorghum panicle were related not only to the potential KW established early in development, as indicated by maximum water content, but also to differences in source availability during the effective grain-filling period. Thus, unlike other cereals, sorghum has the capacity to respond to source increases during late grain filling, as it sets an early sink capacity that is normally not achieved.

3.3. Relevance to yield determination in sorghum

Understanding source and sink limitations on yield formation have important implications for optimizing breeding and management practices. Sorghum kernel growth is

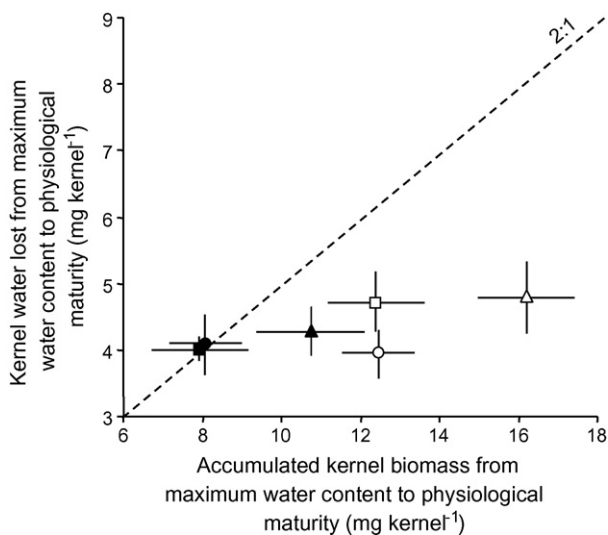


Fig. 7. Relationship between the kernel water lost from maximum water content to physiological maturity and the amount of biomass accumulated during the same period in kernels from apical (closed symbols) and basal (open symbols) positions within the sorghum panicle. Treatments are represented as: circles, untreated control; triangles, increased source per kernel at anthesis; squares, increased source per kernel 15 days after anthesis. Values represent the mean of the seven hybrids, and bars represent the S.E. Both treatments removed 50% of the kernels.

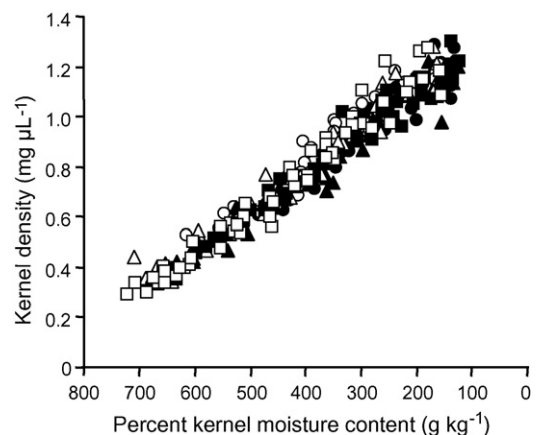


Fig. 8. Relationship between kernel density and percent moisture content during grain filling in kernels from apical (closed symbols) and basal (open symbols) positions within the panicle. Treatments are represented as: circles, untreated control; triangles, increased source per kernel at anthesis; squares, increased source per kernel 15 days after anthesis. Both treatments removed 50% of the kernels. Kernel density was calculated as kernel dry weight (mg kernel^{-1}) divided by kernel volume ($\mu\text{L kernel}^{-1}$).

predominately source limited during most of the grain-filling period, and not sink limited after kernels reach maximum water content. Increased source availability has shown significant increases in sorghum KW, and this response showed to be consistent across environments and genotypes (Fig. 2). Sorghum capacity to continue grain filling and increase the individual KW when source per kernel is enhanced during grain filling is unique among cereals (Borrás et al., 2004). Our findings support the importance of breeding traits (e.g., stay-green genotypes) or management practices (e.g., nitrogen supply) that maintain or improve assimilate availability per kernel during the grain-filling period in this species. When tested, these strategies have shown to enhance sorghum final yield (McBee et al., 1983; Borrell et al., 2000).

Our observation that kernel development is predominately source limited actually helps to explain why current growth models predict with a high level of accuracy sorghum final KW based on the amount of biomass produced per kernel during the effective grain-filling period (Heiniger et al., 1997). This same approach has shown inconsistent results in other cereals like maize (Gambín et al., 2006) or wheat (Aggarwal et al., 1990), whose KW response to changes in assimilate availability per kernel during grain filling differs from the one described for sorghum. In these two species, the final KW is more dependent on the individual kernel sink capacity established early in development (Fischer and HilleRisLambers, 1978; Borrás and Westgate, 2006). As a conclusion, breeding and management practices focusing on improving source production during the latest part of the crop cycle will result in increases in sorghum final yield, bearing in mind that the potential sink size will be set at earlier stages with the number of kernels (Fischer and Wilson, 1975a).

4. Conclusions

Sorghum kernels usually grow under assimilate limited conditions that prevent them from achieving their potential size at physiological maturity. As such, sorghum yield not only depends on the sink size (number of kernels set and the individual kernel sink capacity) established early in grain filling, but also to a great extent on source availability during the effective grain-filling period. The developmental plasticity of sorghum kernels enables the crop to profit from source increases throughout grain filling. This plasticity apparently is related to the capacity of kernels to expand to accommodate the accumulation of water and storage reserves. The understanding of sorghum KW determination raises the issue that although some species reach the maximum water content early in kernel development, this not always defines a temporal limit from where KW (and yield) will not respond to source increases.

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