Published online January 31, 2005

Sorghum Kernel Weight: Growth Patterns from Different Positions within the Panicle

Brenda L. Gambín* and Lucas Borrás

ABSTRACT

The influence of genotype and panicle position on sorghum [*Sorghum bicolor* (L.) Moench] kernel growth is poorly understood. In the present study, sorghum kernel weight (KW) differences during grain filling were analyzed by kernel water relationships previously described in other crops. Eight commercial genotypes differing in KW were used, and KW, water content, kernel volume, kernel moisture content, and kernel density were measured in two positions within the panicle (apical and basal) throughout the grain-filling period. At physiological maturity (PM), KW ranged from 16.5 to 25.1 mg kernel^{-1}, and a significant ($p < 0.05$) genotype × position interaction was detected. Independently of final KW, apical kernels always exhibited a higher rate ($p < 0.001$) and a shorter duration of grain filling ($p < 0.001$) than basal kernels. Maximum water content was related to kernel growth rate but not to final KW. Basal kernels reached maximum kernel volume after attaining maximum water content, with dry matter accumulation affecting kernel volume determination. Kernel density increased with a similar pattern regardless of genotype or panicle position when related to the kernel moisture decline, but at PM, basal kernels were always more dense than apical ones. Differences in the kernel desiccation pattern and in the critical moisture content for biomass accumulation helped explain differences in the grain-filling duration between positions. A general kernel growth curve based on kernel moisture content was impossible to obtain because of the differences in kernel growth patterns within the panicle.

Although it is clear that the number of harvestable seeds per unit area is the dominant yield component in many grain crops, variations in sorghum KW contribute greatly to final yield determination (Stickler and Pauli, 1961; Heinrich et al., 1985; Blum et al., 1997). The pattern of sorghum kernel growth and kernel final weight vary among genotypes as well as among positions in the panicle (Hamilton et al., 1982; Heiniger et al., 1993a,1993b). However, little information exists about the physiological mechanisms controlling these variations. While kernel water relations are useful to understand kernel dry weight differences of some crops (Saini and Westgate, 2000; Borrás et al., 2004), such data in sorghum are lacking.

Early kernel growth involves cellular division and expansion accompanied by water uptake (Egli et al., 1985; Westgate and Boyer, 1986). Once maximum water content is reached, maximum kernel volume is attained (Martínez-Carrasco and Thorne, 1979; Jenner, 1979; Egli, 1990; Saini and Westgate, 2000). Independent of the species, maximum kernel volume is an accurate predictor of final KW (Saini and Westgate, 2000), since final kernel density is essentially constant (Millet and Pinthus, 1984). There is a strong correlation between maximum water content and kernel growth rate in maize (*Zea mays* L.) (Borrás et al., 2003), showing the link between early kernel sink capacity, storage accumulation rates, and final KW. After maximum water content is reached, water is gradually replaced by dry matter deposition, causing gradual kernel desiccation until a critical moisture content that limits biomass deposition (Egli and TeKrony, 1997; Saini and Westgate, 2000). Kernel moisture content declines throughout grain filling (Kersting et al., 1961; Westgate and Boyer, 1986) and has been successfully used to estimate kernel developmental stages defined as the fraction of final KW reached at any time during grain filling. This relationship between moisture content and the stage of kernel development has been described in soybean [*Glycine max* (L.) Merrill] (Swank et al., 1987), wheat (*Triticum aestivum* L.) (Schnyder and Baum, 1992), and maize (Borrás et al., 2003) over a wide range of environmental conditions and genotypes. Because of its simplicity and robustness to estimate the achieved grain-filling stage, kernel moisture content data is currently used as a guide in many crop management practices (Calderini et al., 2000; Calviño et al., 2002).

Genotypic differences in sorghum KW are normally related to changes in the rate of grain filling (Heinrich et al., 1985; Kiniry, 1988). In turn, KW changes in the different positions within the panicle are due to changes in the rate and duration of grain filling (Heiniger et al., 1993a; Kiniry and Musser, 1988). There is still some disagreement in the current literature on the pattern of KW distribution within the panicle. Some authors have demonstrated KW increases from the base to the apex (Fischer and Wilson, 1975; Hamilton et al., 1982; Heiniger et al., 1993a, 1993b), while others have detected the heaviest kernels in basal positions of the panicle (Kiniry, 1988; Kiniry and Musser, 1988). On the other hand, apical kernels always seem to present a higher growth rate (Heiniger et al., 1993a) and a shorter duration of grain filling (Kiniry, 1988; Heiniger et al., 1993a) when compared with the basal ones, but current data is far from conclusive. Because anthesis of the basal section of the panicle is 4 to 10 d later than the apical part, clear definition of the grain-filling period of basal and apical kernels has not been reported. Moreover, only differences in rate are related to the pollination

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Published in Crop Sci. 45:553–561 (2005).

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Abbreviations: KW, kernel weight; PM, physiological maturity; TT, thermal time.

pattern within the sorghum panicle (Heiniger et al., 1993b).

The sorghum genotypes currently used in Argentina have large genotypic differences in final KW, and it has been suggested that this variation is due to differences in kernel volume and density (Trucillo, 2002). Genotypic differences in sorghum kernel density measured after physiological maturity (PM) are well known (Goggi et al., 1993). Data from Kiniry and Musser (1988) support the observation that genotypes may differ in kernel density during grain filling as well as the possibility that kernels coming from different positions within the sorghum panicle may also have differences. If variations in kernel density were the normal case in sorghum, maximum water content (as a maximum volume estimator) would not serve as an early KW predictor when different genotypes or positions within the sorghum panicle are considered. Thus, the objectives of the present work were to study (i) if variations in final KW due to genotypes or positions within the panicle are explained by differences in kernel growth rate or in duration of grain filling, (ii) whether KW changes among genotypes or positions are correlated with water content (or volume) established early in development, and (iii) the possibility of establishing a general kernel developmental curve for all genotypes and positions on the basis of kernel moisture content values.

MATERIALS AND METHODS

The experiment was conducted in the field of the Department of Plant Production, University of Buenos Aires (35°35′ S, 59°29′ W), on a silty clay loam soil (Aeric Argiudol). Eight current Argentine commercial genotypes (DA48, DK51, DK68T, X7761, Relámpago 20R, 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 (urea) was applied twice: before sowing (70 kg N ha^{-1}) and post-emergence (100 kg N ha^{-1}) between the four- 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 to 10 d after the apical section. Apical and basal anthesis dates were recorded in 30 marked plants per replicate by dividing the panicle into four equal sections on the basis of the number of whorls on the rachis (Heiniger et al., 1993a, 1993b). Beginning at apical anthesis, the panicle of one plant per replicate was harvested every 3 to 5 d. The panicle was immediately enclosed in a tight plastic bag and transported to the lab 150 m away. Twenty-five kernels from positions 1 and 4 (Heiniger et al., 1993a, 1993b) were sampled for fresh and dry weight determination. Sampling was done in a humidified box to prevent water loss (Westgate and Boyer, 1986; Borrás et al., 2003). Fresh weight was measured immediately, and 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 kernel moisture (g kg^{-1}) during grain filling. Fifteen days after apical anthesis, 10 to 15 kernels taken from each position of the same harvested panicles were used to determine kernel volume by volumetric displacement in a pipette (Martínez-Carrasco and Thorne, 1979; Kiniry, 1988). Kernel density (mg μL^{-1}) was calculated as the ratio between kernel dry weight (mg $kernel^{-1}$) and kernel volume (μL $kernel^{-1}$).

Final KW, kernel growth rate, duration of the lag phase and duration of the whole grain-filling period for each genotype and position were determined by fitting a trilinear model (Eq. [1], [2], and [3]):

$$KW = a + b\,TT \text{ for } TT <= c \qquad [1]$$

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

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

where KW is kernel weight, TT is thermal time after anthesis, a is the y-intercept (mg), b is the kernel growth rate during the lag phase (mg $°Cd^{-1}$), c is the duration of the lag phase (°Cd), d is the kernel growth rate during the effective grain-filling period (mg $°Cd^{-1}$), and e is the total duration of grain filling (°Cd). The trilinear model was fitted to the kernel dry weight data by the iterative optimization technique in Table Curve V 3.0 (Jandel Scientific, 1991). Daily TT values were obtained with 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 TT after anthesis for each sample was always referred to its own apical or basal anthesis date.

Moisture content value at PM was determined by a bilinear model relating kernel dry weight and kernel moisture content data (Eq. [4] and [5]), using the iterative optimization technique in Table Curve V 3.0 (Jandel Scientific, 1991):

$$KW = f - g\,Mc \text{ for } Mc >= h \qquad [4]$$

$$KW = f - gh \text{ for } Mc < h \qquad [5]$$

where KW is kernel weight, Mc is moisture content (in g kg^{-1}), f is the y-intercept (mg), g is the rate of kernel moisture decline during grain filling [mg (g $kg^{-1})^{-1}$], and h is the critical moisture content at PM (g kg^{-1}).

Maximum water content and maximum kernel volume were considered as the maximum values registered in each replicate of genotype × position combination. Differences among genotypes and positions in all measurements were determined by ANOVA as a split plot design, with genotypes as main plots and panicle positions as sub-plots.

RESULTS

Kernel Weight Differences between Genotypes and Positions within the Panicle

The genotypes differed in flowering date and in the mean time between apical and basal anthesis (Fig. 1). Apical or basal anthesis of the first flowering genotype was 8 to 9 d before the last genotype. Within each genotype, anthesis of the basal part of the panicle was 2 to 4 d after apical anthesis.

There was a wide range of KWs at PM because of genotypic differences ($p < 0.001$) as well as to differences because of positions within the sorghum panicle ($p < 0.01$; Table 1). Kernel weight among genotypes

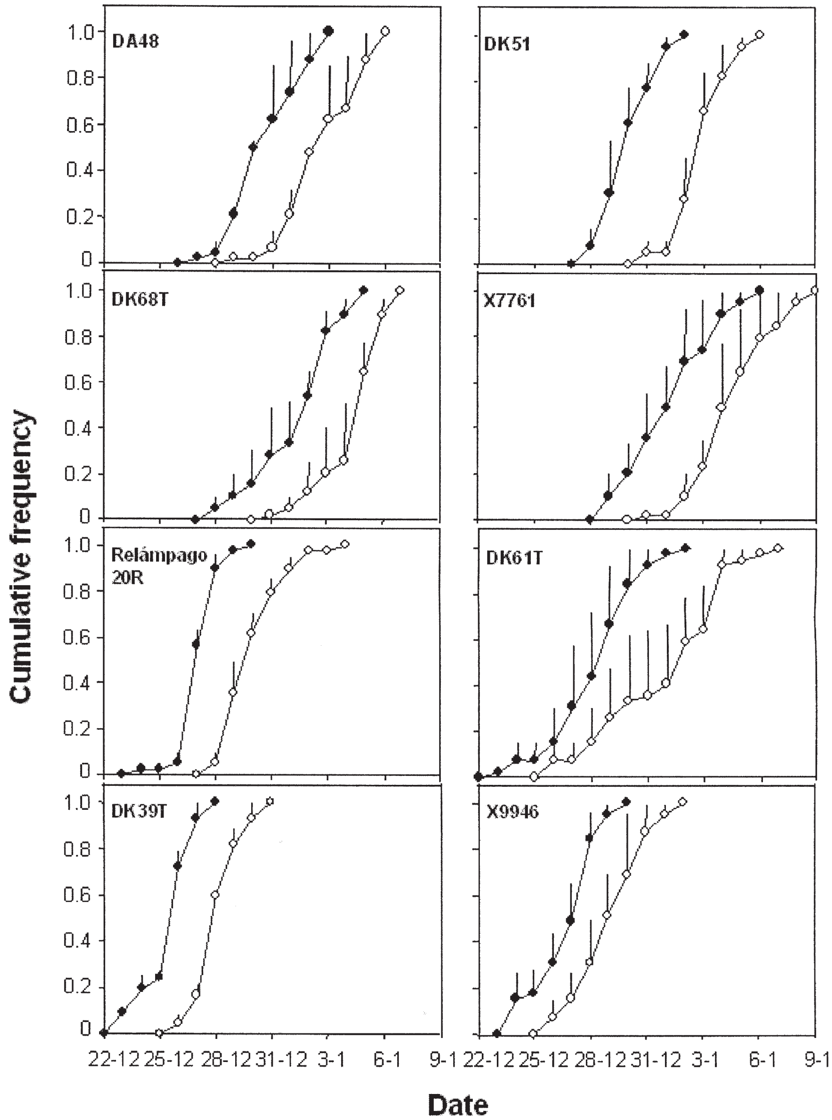

Fig. 1. Cumulative frequency of plants reaching apical (closed symbols) and basal (open symbols) panicle anthesis from the eight genotypes tested in the present work. Bars represent the SE of the mean of three replicates of 30 plants each.

ranged from 16.5 to 23.5 mg kernel^{-1} in the apical position, and from 17.8 to 25.1 mg kernel^{-1} in the basal position (Table 1). Kernel weight variations due to genotypic differences were registered in both panicle positions, as there was a significant relationship ($r^2 = 0.62$; $p < 0.05$; $n = 8$) between apical and basal KW within genotypes. However, there was a significant genotype × position interaction ($p < 0.05$) in final KW, showing no consistent position effect on KW (Table 1).

Kernel growth rate was the most important factor affecting final KW of the different genotypes ($r^2 = 0.71$; $p < 0.01$; Fig. 2A). Genotypic differences in final KW observed at PM were not related to the duration of the grain-filling period ($r^2 = 0.20$; $p < 0.14$; Fig. 2B). However, if genotype DK61T is excluded from the analyze, final KW was also related to the duration of grain filling ($r^2 = 0.62$; $p < 0.01$; $n = 7$), showing that both kernel growth rate and duration of grain filling were associated with genotypic differences in final KW.

Kernel position within the panicle generated great differences in the pattern of kernel growth independently the genotypic differences observed in final KW. Basal kernels always had a lower rate of grain filling during the effective grain-filling period compared with the apical ones ($p < 0.001$; Table 1). Averaging all genotypes, kernel growth rate of the basal kernels was 68% of the rate observed in apical kernels (3.5 vs. 5.2 mg 10^{-2} °Cd^{-1} for basal and apical kernels, respectively). However, because the duration of the grain-filling period of the basal kernels was always significantly longer than the apical ones ($p < 0.001$), final basal KW was equal to or higher than apical KW (Table 1). Averaging across genotypes, the total grain-filling duration of apical kernels was 71% of the basal grain-filling duration (505 vs. 707°Cd for apical and basal kernels, respectively). This longer grain-filling duration of the basal kernels was not caused by a longer duration of the lag phase (Table 1), which remained very stable across genotypes and positions. Clearly, basal kernels had a longer duration of the effective grain-filling period when com-

Table 1. Final KW, total duration of the grain-filling period, duration of the lag phase, kernel growth rate during the effective grain-filling period, maximum water content, maximum kernel volume, and thermal time (TT) during grain filling when maximum kernel volume was attained, in all genotypes and the two positions within the panicle considered in the present study. Statistical analysis determined by ANOVA ($n = 3$).

Genotype	Position	Kernel weight	Thermal time duration: Grain-filling period	Thermal time duration: Lag phase	Kernel growth rate	Maximum water content	Maximum kernel volume	TT at maximum kernel volume
		mg kernel^{-1}	°Cd	°Cd	mg 10^{-2} °Cd^{-1}	mg kernel^{-1}	μL kernel^{-1}	°Cd
DA48	apical	21.3	536	97	4.9	17.3	27.3	389
	basal	21.4	665	120	3.7	14.9	28.0	731
DK51	apical	19.9	465	111	5.4	14.8	26.3	418
	basal	20.4	693	97	3.4	12.0	21.7	656
DK68T	apical	22.3	523	118	5.3	16.5	30.1	392
	basal	21.6	714	115	3.5	13.3	26.9	674
X7761	apical	23.5	490	121	6.3	18.4	30.9	552
	basal	25.1	761	119	4.0	14.8	28.5	869
Relámpago 20R	apical	20.1	521	121	4.8	15.3	25.9	447
	basal	23.8	750	94	3.7	13.0	27.0	725
DK61T	apical	16.5	514	137	4.8	15.3	24.1	456
	basal	17.8	701	47	2.7	11.1	22.2	508
DK39T	apical	21.8	504	138	5.8	17.8	29.7	490
	basal	21.9	761	112	3.3	13.8	25.5	680
X9946	apical	18.5	493	100	4.7	15.2	24.8	444
	basal	20.0	611	112	3.9	12.4	23.7	703
Genotype (G)		*** (2.4)†	NS	NS	NS	*** (1.3)	** (3.5)	NS
Position (P)		** (0.6)	*** (47)	NS	*** (0.5)	*** (0.6)	* (1.6)	*** (85)
G x P		* (1.6)	NS	NS	NS	NS	NS	NS

* Significant at $P = 0.05$.
** Significant at $P = 0.01$.
*** Significant at $P = 0.001$.
NS = not significant.
† LSD value for $P \leq 0.05$.

pared with apical kernels. The precise flowering notes taken for each panicle position were important in understanding this fact, as each panicle section was always referred to its own anthesis date.

Water Relations and Kernel Weight Differences

Genotypes differed in the maximum water content attained at mid-grain filling ($p < 0.001$), and kernel position also affected maximum water content ($p < 0.001$; Table 1). Apical kernels always reached higher values of maximum water content compared with basal ones. Averaging all genotypes, maximum water content was 16.3 and 13.1 mg kernel^{-1} in apical and basal kernels, respectively.

When all genotypes and positions were considered, variations in final KW were not related to the maximum water content attained at mid-grain filling (Fig. 3A). However, a significant correlation existed between maximum water content and final KW for each position within the panicle (Fig. 3A). Apical and basal kernels had different ranges of maximum water content but were similar in final KW. On the other hand, the maximum water content was strongly related to the rate of grain filling ($r^2 = 0.80$; $p < 0.001$; Fig. 3B) independently of the genotype or the panicle position. There was no apparent relationship between maximum water content and the duration of grain filling (Fig. 3C).

Apical and basal kernels exhibited different patterns in the change of water content during the latter part of the grain-filling period, and this was independent of their maximum water content (Fig. 4B; Table 1). As shown in Fig. 4B, both positions reached maximum water content at the same TT after anthesis, but there were differences in the pattern of water content decline during late grain filling. Water content of apical kernels always declined at a faster rate than that of the basal ones.

Maximum kernel volume was affected by the genotype ($p < 0.01$) and the position within the sorghum panicle ($p < 0.05$; Table 1). Differences in maximum kernel volume between genotypes were related to genotypic differences in final KW ($r^2 = 82$; $p < 0.005$; $n = 8$). Differences in kernel volume between panicle positions were related to the maximum value reached and to the pattern of volume development in all the genotypes tested. Apical kernels reached higher kernel volume values ($p < 0.05$) and earlier in development when compared with basal kernels ($p < 0.001$; Table 1). Apical kernels reached maximum water content and maximum volume at the same time during grain filling, while basal kernels attained maximum water content before maximum volume was achieved (Fig. 4B and C). This indicates that dry matter deposition is as important as water content for volume determination in sorghum kernels. Also, although the maximum water content was significantly correlated to the maximum kernel volume ($r^2 = 0.60$; $p < 0.001$), the maximum water content could not accurately predict the final kernel volume. When all genotypes and positions were pooled together, the final KW was related more to the volume attained at PM ($r^2 = 0.60$; $p < 0.001$; $n = 16$) than to the maximum volume attained at any time during grain filling ($r^2 = 0.45$; $p < 0.01$; $n = 16$).

Kernel moisture content declined throughout grain filling (Fig. 4D). No differences were observed among genotypes at both positions of the sorghum panicle, but

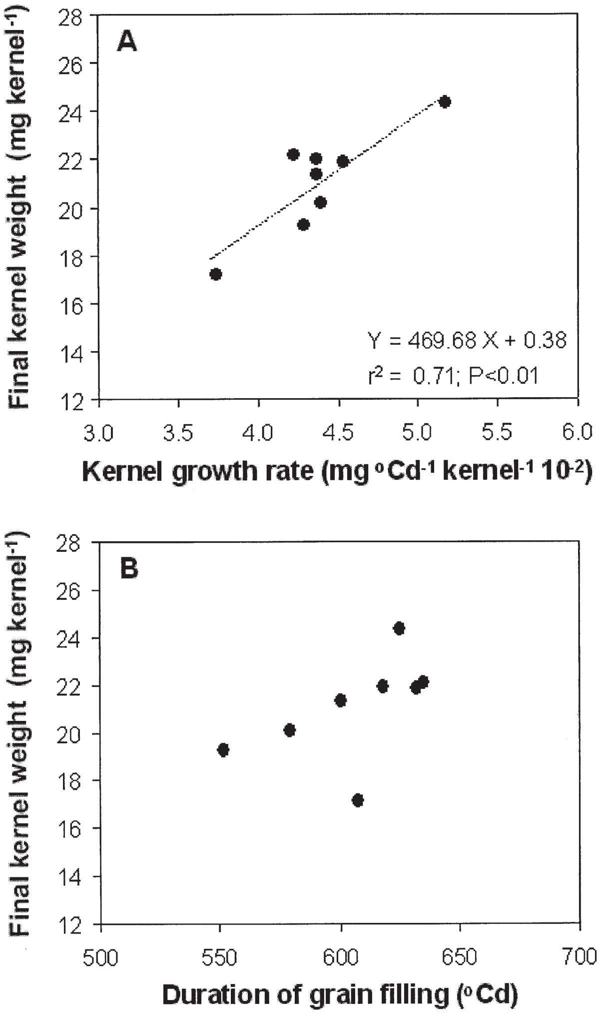

Fig. 2. Relationship between mean final kernel weight and kernel growth rate (A) and total duration of grain filling (B) for the eight genotypes tested.

significant differences were detected between positions (Fig. 4D). Basal kernels showed a slower kernel desiccation at the end of grain filling, probably related to the previously noted slower water content decline (Fig. 4B). At the same time, basal kernels always reached maximum KW with a lower moisture content value than apical ones ($p < 0.001$; Table 2). Averaging across all genotypes, moisture content at PM was 364 and 279 g kg^{-1} for apical and basal kernels, respectively. This lower critical moisture content for biomass deposition in basal kernels was significantly correlated to their longer duration of grain filling ($r^2 = 0.79$; $p < 0.001$; Fig. 5) when compared with the apical ones.

Moisture content allowed an estimate of the percentage of final KW achieved by any genotype during the grain-filling period, but this relationship depended on the kernel position within the panicle (Fig. 6A). Although the primary difference was the critical moisture content at PM between positions, differences around 40 to 60% moisture content were also evident during grain filling, showing a different growth pattern. Also, both positions reached maximum water content at similar values of kernel moisture content (Fig. 6B), but maxi-

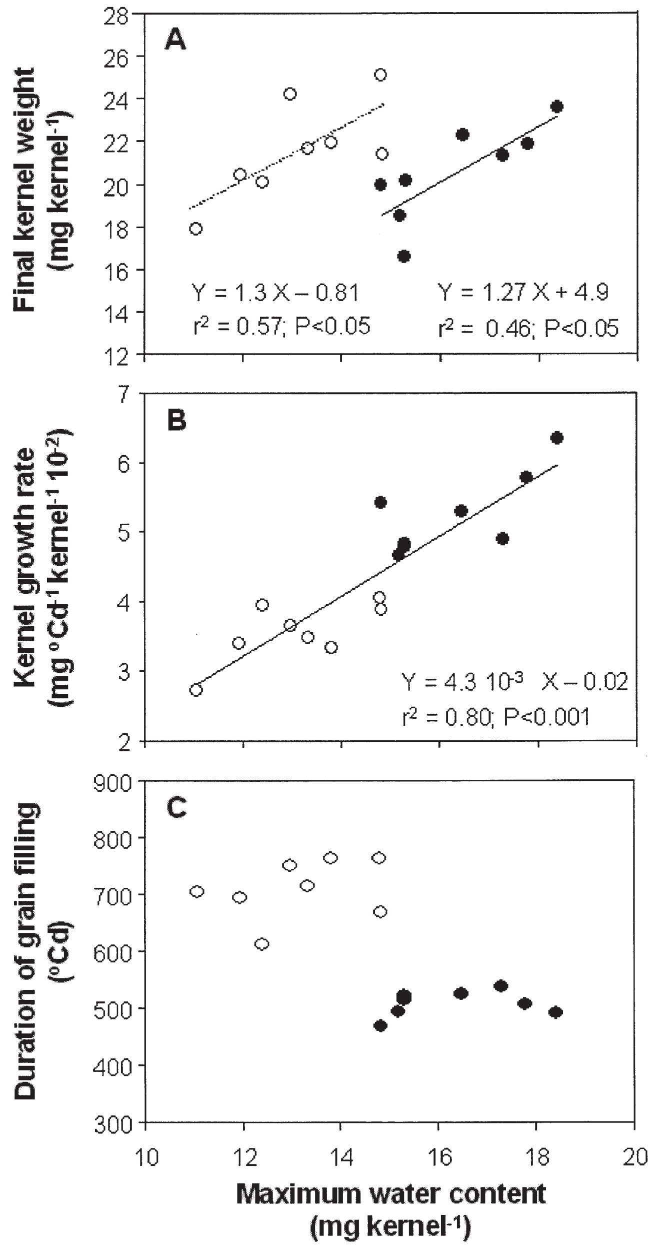

Fig. 3. Relationship between final kernel weight (A), kernel growth rate (B), and duration of the grain-filling period (C) and maximum water content in apical (closed symbols) and basal (open symbols) kernel positions within the sorghum panicle, for all the genotypes tested. Final kernel weight was calculated by a trilinear with plateau model, and maximum water content was determined as the maximum value measured in each genotype × position combination.

mum kernel volume in basal kernels was reached at lower moisture contents than in apical ones (Fig. 6C). Thus, basal kernels not only reached maximum kernel volume at a later TT compared with apical kernels, but also with a lower kernel moisture content ($p < 0.001$; Table 2).

Kernel density showed a stable increase when related to kernel moisture content decline throughout grain filling, with no differences between genotypes or panicle positions (Fig. 7). However, as apical kernels reached PM with a higher kernel moisture content when com-

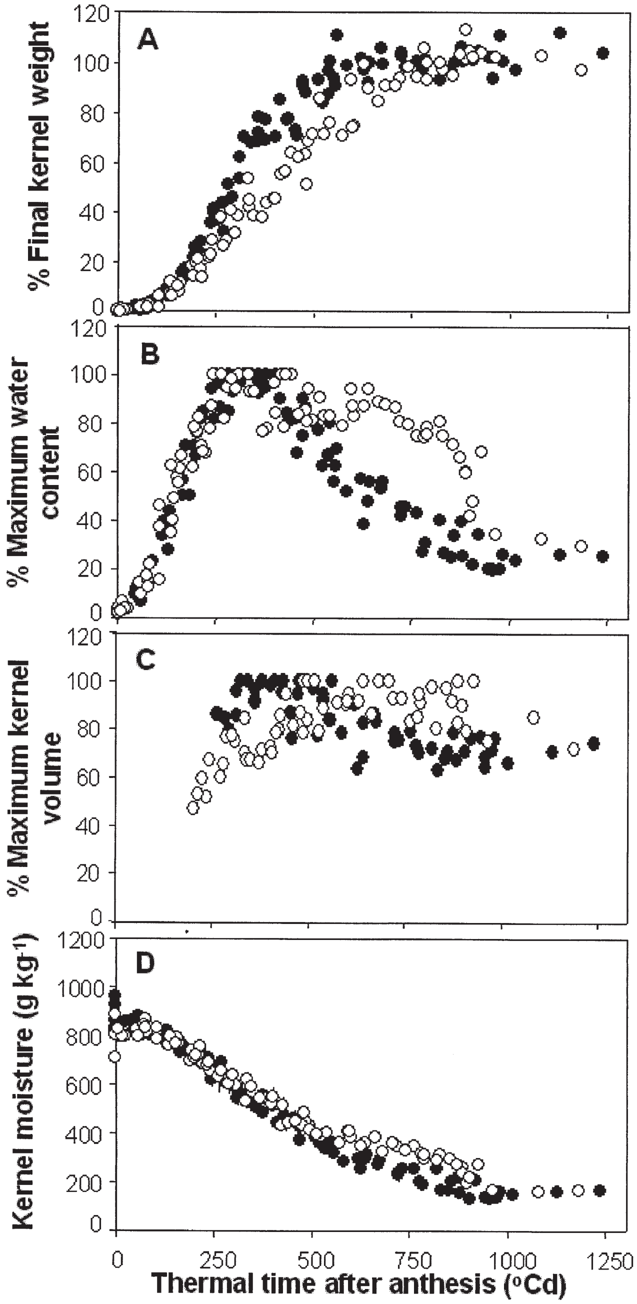

Fig. 4. (A) Relative final kernel weight, (B) relative maximum water content, (C) relative maximum kernel volume, and (D) kernel moisture in apical (closed symbols) and basal (open symbols) kernel positions within the panicle for all the sorghum genotypes evaluated. In 4D, bars represent the SE of the mean of three replicates.

pared with the basal ones (Table 2; Fig. 5), apical kernels reached PM with lower kernel density values.

DISCUSSION

Sorghum kernel growth differs depending on its position within the panicle. Independent of genotypic differences in final KW, we found differences in both kernel growth rate and total duration of grain filling between the two extreme panicle positions. Apical kernels always

Table 2. Kernel moisture content during grain filling when kernels reached physiological maturity and when they reached maximum kernel volume, in all the genotypes and the two positions within the panicle considered in the present study. Statistical analysis determined by ANOVA (n = 3).

Genotype	Position	Moisture content: At physiological maturity	Moisture content: At maximum kernel volume
		g kg^{-1}	
DA48	apical	362	526
	basal	316	332
DK51	apical	372	433
	basal	281	329
DK68T	apical	380	520
	basal	304	366
X7761	apical	378	363
	basal	241	293
Relámpago 20R	apical	324	435
	basal	229	371
DK61T	apical	396	481
	basal	292	423
DK39T	apical	364	434
	basal	276	369
X9946	apical	338	426
	basal	293	329
Genotype (G)		NS	NS
Position (P)		*** (17)†	*** (51)
G x P		NS	NS

*** Significant at P = 0.001.
NS = not significant.
† LSD value for $P \leq 0.05$.

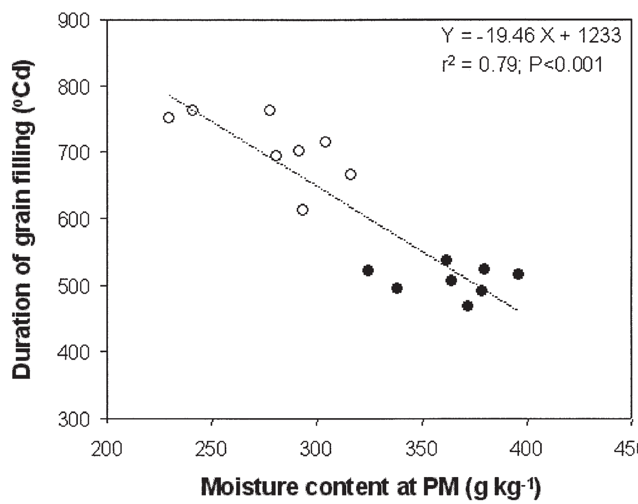

Fig. 5. Relationship between the total duration of the grain-filling period and kernel moisture content at physiological maturity (PM) in apical (closed symbols) and basal (open symbols) kernel positions within the panicle for all the genotypes tested.

had a higher growth rate during the effective grain-filling period than basal kernels (Table 1), in accordance with previous studies (Heiniger et al., 1993a, 1993b; Kiniry, 1988). In turn, total duration of grain filling was always longer in basal kernels, and this was not related to a phenological delay in flowering time. The longer grain-filling duration of late appearing structures differs from what has been typically found in other species. In maize, apical kernels coming from late appearing silks have a shorter duration of grain filling than first appearing basal kernels, allowing all kernels from the same spike to reach PM synchronously (Tollenaar and Daynard, 1978). This also occurs in soybean, where there

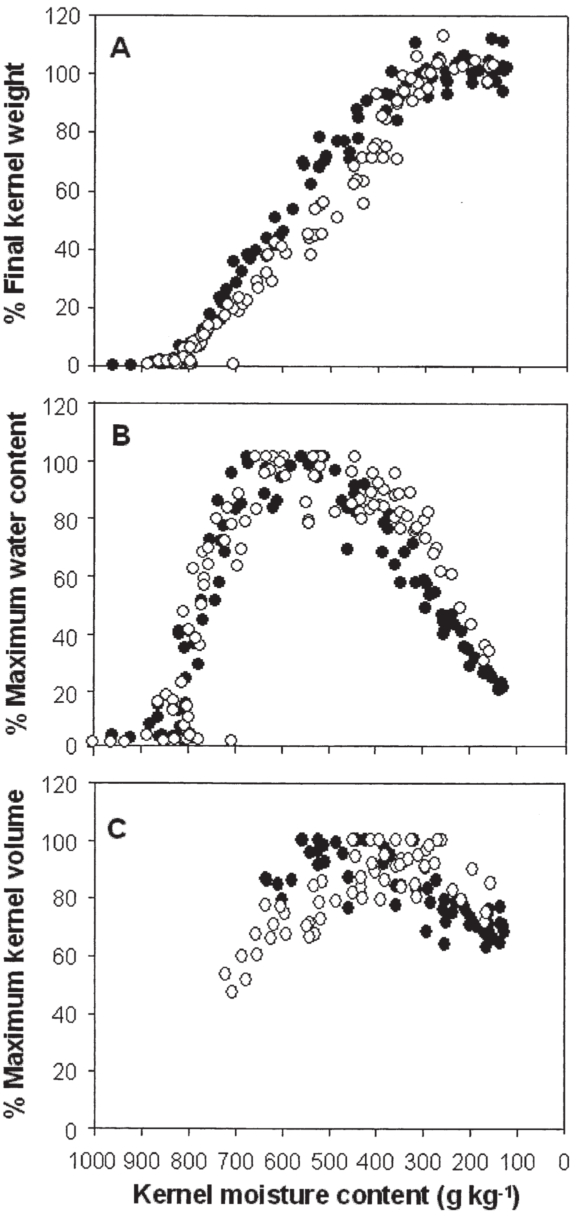

Fig. 6. Relationship between relative maximum kernel weight (A), relative maximum water content (B), and relative maximum kernel volume (C) with moisture content during grain filling in apical (closed symbols) and basal (open symbols) kernel positions within the panicle for all the genotypes evaluated.

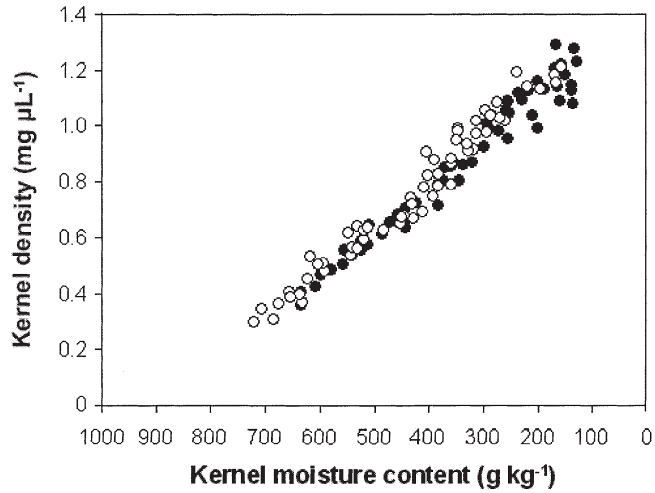

Fig. 7. Relationship between kernel density and moisture content during grain filling in apical (closed symbols) and basal (open symbols) kernel positions within the panicle for all the genotypes tested. Kernel density was calculated as kernel dry weight (mg kernel^{-1}) divided by kernel volume (μL kernel^{-1}).

are greater differences between early and late appearing pods in the initiation of seed growth than there are in the time early or late seeds reach PM (Egli et al., 1978).

Independent of the kernel location within the sorghum panicle, the rate of grain filling was strongly related to the maximum water content kernels reached (Fig. 3B). This relationship has been found in maize kernels coming from different growing conditions (Borrás et al., 2003) and can be found in soybean data with genotypic differences in final seed dry weight (Swank et al., 1987) or growing in in vitro conditions (Egli, 1990). However, the total duration of grain filling was independent of the maximum water content kernels achieved, and clearly differed between positions (Fig. 3C). Thus, maximum water content was not a good predictor of final KW in sorghum, when all genotypes and sections of the panicle were considered. The relationship between maximum water content and final KW shown by several authors in other species (Millet and Pinthus, 1984; Saini and Westgate, 2000; Borrás et al., 2003) could not be generalized to sorghum kernels.

Differences in duration of grain filling between panicle positions seemed to be related to changes in kernel desiccation pattern (Fig. 4 and 5). Previous work in soybean has shown that the time when maximum water content is attained determines the seed-filling duration because it establishes the period seed moisture content remains above a critical value (Egli, 1990). The present work in sorghum showed kernel desiccation pattern as another mechanism affecting the duration of grain filling (Fig. 4). Kernels from different positions not only differed in the development of water content after the maximum value was reached (Fig. 4B), but also in the critical moisture content at which final KW was attained (Fig. 5). On the basis of this, we conclude that potential KW depends not only on maximum water content, as suggested by several authors (Egli, 1990; Saini and Westgate, 2000; Borrás et al., 2003), but also on the kernel desiccation pattern. These differences found in kernel desiccation were previously shown in soybean seeds growing with a physical restraint (Egli et al., 1987). In this case, where limited water uptake occurred, the seed capacity to delay water loss established a higher duration of grain filling than the one predicted by the time maximum water content was attained (Egli, 1990). We currently hypothesize that differences in sorghum kernel desiccation, resulting in the capacity to achieve a higher KW than the one expected from maximum water content, may help explain the large increases in KW that were achieved by enhancing the source–sink ratio during late grain filling (Fischer and Wilson, 1975; Heiniger et al., 1993a), together with the high KW plasticity this crop has shown (Stickler and Pauli, 1961; Fischer and Wilson, 1975; Muchow and Wilson, 1976).

There have been no previous studies showing how kernel density increases during grain filling, only studies focusing on single measurements at different moments throughout the grain-filling period (Millet and Pinthus, 1984; Kiniry and Musser, 1988). This study in sorghum indicates that kernel density has a stable increment when related to the kernel moisture content decline during grain filling, not only in different positions in one genotype but also across genotypes (Fig. 7). In spite of this stable increase, kernel density at PM differed between panicle positions, since they reached final KW with different kernel moisture contents (Table 2). The differences in seed density between genotypes and positions that can be depicted from Kiniry and Musser (1988) are likely to be related to different kernel developmental stages at the moment of sampling. As shown in the present study, when different positions were compared, there was no relationship between the thermal time (Fig. 4) or the kernel moisture content (Fig. 6) at which kernel maximum water content and volume were achieved. Dry matter accumulation, together with a slower water content decline, caused the volume of basal kernels to increase at lower kernel moisture contents (Fig. 6C). This is different from what has been observed in other species (Egli, 1990; Saini and Westgate, 2000), where the kernel's ability to continue water accumulation seemed to be critical for cellular expansion and volume determination. In agreement with results from Kiniry (1988), sorghum kernel sink capacity is not determined by the physical size of the endosperm set early in development, as shown with the kernel growth pattern of apical and basal kernels.

In sorghum, the link between water content and dry matter shown in other species was partially maintained because of differences in the growth pattern of apical and basal kernels. Kernel developmental stage of all the genotypes tested could be estimated from kernel moisture content after taking into consideration the panicle position where kernels came from. We found that it is not possible to generate a single curve for sorghum, as has been shown in wheat (Schnyder and Baum, 1992; Calderini et al., 2000), soybean (Swank et al., 1987), and maize (Borrás et al., 2003). One reason may be that this study deals with water relations of kernels coming from different parts of the inflorescence. Further studies are necessary to define the processes that regulate the behavior of kernels from different positions within the reproductive structures.

CONCLUSIONS

The pattern of kernel growth differed depending on the position within the sorghum panicle, and this was independent of genotypic differences in final KW. Apical kernels had higher growth rates, shorter effective grain-filling periods, higher maximum water contents and greater maximum volumes than basal kernels. Basal kernels had the capacity to achieve equal or greater KW when compared with apical kernels by having a different desiccation pattern, which allowed maximum volume to occur latter than maximum water content. Although there were very different kernel growth patterns because of genotypes and positions within the panicle, kernel density increased in a similar manner throughout grain filling when related to the kernel moisture content decline. A general kernel growth curve based on kernel moisture content was impossible to achieve because of the differentially regulated kernel growth patterns within the panicle.

ACKNOWLEDGMENTS

The authors wish to thank M.E. Otegui and V. Trucillo for valuable help and suggestions, G. Paván and F.L. Lo Valvo for help in field data collection, J.R. Schussler for critically reading the manuscript, and H.J. Earl for his detailed revision of the manuscript. L. Borrás held a post-graduate scholarship from CONICET, the Research Council from Argentina.

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