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Kernel weight dependence upon plant growth at different grain-filling stages in maize and sorghum

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Abstract. In the present study we tested how assimilate availability per kernel at different grain-filling stages may affect maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L. Moench) individual kernel weight (KW). These two species have shown a contrasting KW response to increased assimilate availability at similar seed developmental stages. Plant growth rate (PGR) per kernel was used to estimate the assimilate availability per kernel at two stages: around the early grain-filling period when kernel number per plant is also being established, and around the effective grain-filling period. We tested 3 commercial genotypes from each species, and modified the PGR by thinning or shading the stand at different developmental stages. In both species, each genotype showed a particular relationship between PGR around flowering and kernel number, which gave a range of responses in the PGR per kernel set around flowering. Final KW always increased whenever PGR per kernel around flowering was enhanced. Only sorghum showed a consistent KW increase when PGR per kernel during the effective grain-filling period was enhanced. Results confirmed that increasing assimilate availability per kernel will affect maize kernel size only if the potential set early in development is altered. Most important, we showed that linking specific KW sensibility across species at different seed developmental stages using a simple estimate of assimilate availability per seed (i.e. PGR per kernel) at each grain-filling stage helped explain most of the explored genotypic and environmental variability in final kernel size.

Additional keywords: *Zea mays* L, *Sorghum bicolor* L. Moench, source–sink relations, potential sink size, genotypes.

Introduction

Identifying crop developmental stages when yield components respond to plant growth changes is important for guiding breeding and management efforts aimed to increase yield. Responses of kernel weight (KW) to changes in assimilate availability per kernel at similar timings of post-flowering stages seem different in maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L. Moench) (Borrás *et al*. 2004; Gambín and Borrás 2007). Hence, we conducted a series of comparative experiments to determine how both species determine their KW at maturity when conditions at different crop developmental stages are altered.

The grain-filling period is usually divided in three phases (Bewley and Black 1985). The first one, known as the *lag* phase, occurs after ovary fertilisation. It is a period of active cell division, characterised by a rapid increase in kernel water content, with almost no dry-matter deposition. This phase is critical for establishing the potential kernel size and subsequent kernel growth rate, because sites for subsequent reserve deposition are set during this period (Brocklehurst 1977; Capitano *et al*. 1983; Reddy and Daynard 1983; Jones *et al*. 1996). The second phase, known as effective grain-filling period, is characterised by a rapid increase in the rate of biomass deposition. Kernel water content continues to increase and reach a maximum value close to mid grain filling, after which it declines. The third phase starts when reserve deposition is arrested. This stage is known as physiological maturity. From this stage onwards, kernels continue losing water content, but dry weight remains stable.

In maize, variations in KW are highly dependent upon the potential established during the early grain-filling stages (Capitano *et al*. 1983; Reddy and Daynard 1983; Jones *et al*. 1996; Borrás and Westgate 2006). This period overlaps with the period when plants are adjusting their kernel number to the plant source availability (Andrade *et al*. 1999). This implies that the crop is adjusting the number of kernels and the potential kernel size at the same time. Based on the typical curvilinear relationship between kernel number per plant and plant growth rate (PGR) around flowering (Edmeades and Daynard 1979; Andrade *et al*. 1999; Vega *et al*. 2001), Gambín *et al*. (2006) proposed to use the PGR per set kernel for estimating the potential assimilate availability per established kernel. Because of this curvilinear relationship, the intrinsic efficiency of the maize plant to set kernels changes as PGR around flowering increases (Andrade *et al*. 1999, 2002). Hence, the growing conditions around flowering modify the number of kernels and the amount of assimilates available per kernel during early grain filling, affecting the potential kernel size (Gambín *et al*. 2006). The hypothesis that variations in PGR per kernel could be sensed directly by growing kernels is supported by

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current knowledge on phloem unloading and transport events from source to sink (Patrick 1997). Changes in assimilate production by leaves (source) directly affect assimilate availability to developing kernels (sink) by increasing the pressure difference that governs photoassimilate movement (Patrick 1997). Hence, an increased PGR per kernel during early grain filling would modify the amount of assimilates available for developing kernels at the developmental stage when potential kernel size is established.

Maize genotypes differ in their growth around flowering, and in their efficiency for setting kernels at similar PGRs (Fig. 1*a*; Tollenaar *et al*. 1992). This can affect the PGR per kernel during the early stages of kernel development (Fig. 1*b*). We hypothesise that our estimate of assimilate availability per kernel early in grain filling (PGR per kernel) should explain differences in final KW (Fig. 1*c*), because maize kernels normally grow close to saturated assimilate availability conditions during the effective grain-filling period (Borrás *et al*. 2004). We expect final KW and PGR per kernel during the effective grain-filling period to show no consistent relationship. Using a set of 12 commercial hybrids, Gambín *et al*. (2006) showed that genotypic differences in mean kernel growth rate and final KW were correlated with differences in PGR per kernel around flowering, and not with the PGR per kernel during the effective grain-filling period. Increasing assimilate availability per kernel during the effective grain-filling period has shown almost null increases in final kernel size (Borrás *et al*. 2004), and reducing this availability limits achieving the early established potential (Borrás *et al*. 2004; Borrás and Westgate 2006). Hence, Fig. 1*d* shows the hypothetical response of final KW to variations in PGR per kernel during the effective grain-filling period for a particular genotype.

Various sources of evidence suggest that sorghum determines KW differently from maize when analysed within a similar framework. Firstly, kernel number is linearly related to PGR around flowering (Fig. 1*e*; Gerik *et al*. 2004). Genotypes can differ in their PGR around the kernel set period and in the efficiency for setting kernels (Fig. 1*e*), but this linear relationship should indicate early assimilate availability per kernel to be constant within each genotype across growing conditions (Fig. 1*f*). This implies that differences in PGR around flowering would give similar potential KWs, and we hypothesise differences in potential size to be related to variations in PGR per kernel around flowering (Fig. 1*g*). Secondly, during the effective grain-filling period, sorghum kernels grow below the assimilate availability conditions that maximise the potential size (Gambín and Borrás 2007). This makes KW respond to increases in PGR per kernel during late grain-filling stages (Fig. 1*h*; Heiniger *et al*. 1997). As in maize, reducing assimilate availability per kernel during the effective grain filling will reduce final KW (Fig. 1*h*; Blum *et al*. 1997).

The main objective of this study was to evaluate the responsiveness of KW to differences in PGR per kernel at early and mid phases of grain filling. Figure 1 shows a graphical representation of our working hypothesis. To test this we used 3 commercial genotypes from each species and manipulative treatments to modify the PGR per kernel around flowering and during the effective grain-filling period. Examining the response of individual plants within the population, rather than population

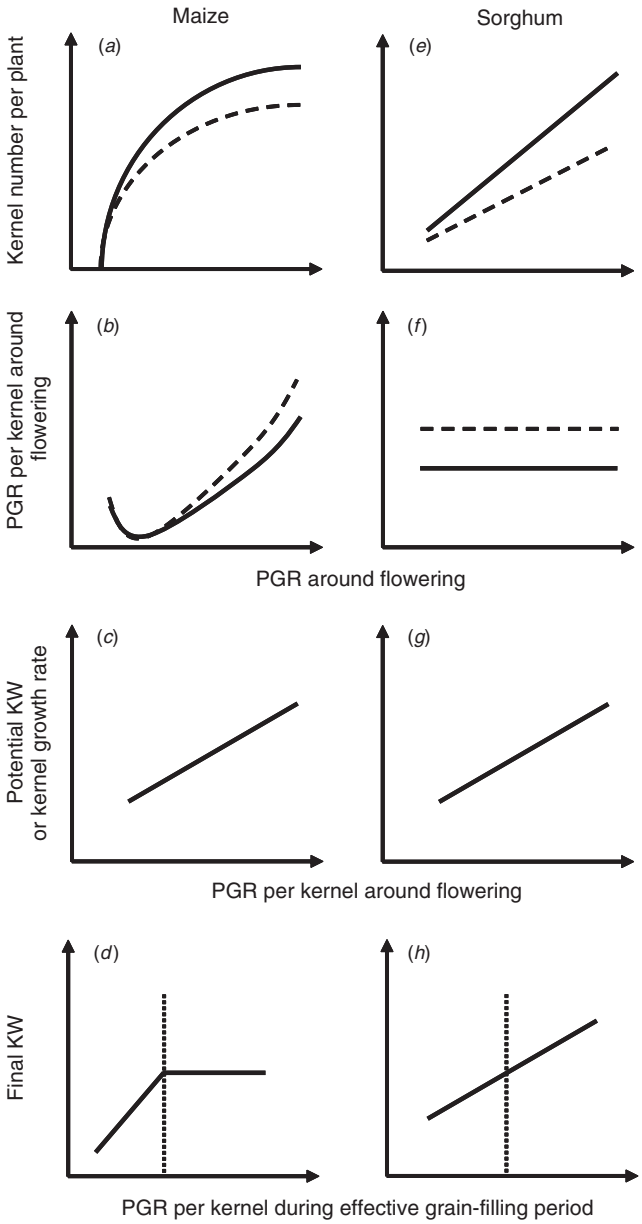

Fig. 1. Diagrams illustrating our working hypothesis for understanding kernel weight (KW) determination using a plant biomass approach for (*a*, *b*, *c*, *d*) maize and (*e*, *f*, *g*, *h*) sorghum. (*a*, *e*) Expected relationship between kernel number per plant and plant growth rate (PGR) around flowering; (*b*, *f*) relationship between PGR per kernel around flowering and PGR around flowering; (*c*, *g*) relationship between potential KW or kernel growth rate and PGR per kernel around flowering; (*d*, *h*) relationship between final KW and PGR per kernel during the effective grain-filling period. The full line represents a genotype with a higher biomass partitioning to the ear or panicle around the kernel set period, and the dashed line represents a genotype with a lower reproductive biomass partitioning around the same period. The relationships shown in *c*, *d*, *g* and *h* are the same for the 2 genotypes differing in reproductive partitioning. The dotted line in figure panels *d* and *h* indicates the source conditions under which kernels are normally set to grow during late grain filling.

averages, enables us to quantify the response to a much greater range of PGRs (Vega *et al*. 2001). As such, we also applied an individual plant basis approach.

Materials and methods

Experiments were conducted in the experimental field of the Department of Plant Production at the University of Buenos Aires (35°35′S, 59°29′W) during the 2004–05 (Expt I), 2002–03 (Expt II) and 2005–06 (Expt III) growing seasons. Soils were of the silty clay loam type (Vertic Argiudoll). In Expt I, 2 maize genotypes (hybrids A×888 CL-MG and A×842 MG; Nidera Argentina 2003) were sown on 8 October at a stand density of 9 plants/m^2. In Expt II, the maize hybrid DK682 (Monsanto Argentina 2003) was sown on 23 September at a stand density of 10 plants/m^2. Details from Expts I and II have been previously described in Gambín *et al*. (2007). In Expt III, 3 commercial sorghum genotypes differing in plant height (hybrids X9946, X7761, and DK68T; Monsanto Argentina 2003) were sown on 19 October at a stand density of 20 plants/m^2.

In all experiments, treatments were arranged in a randomised complete block design with 3 replicates. Each replicate involved 5 rows, 4 m long and 0.5 m apart (Expt I); 10 rows, 4 m long and 0.7 m apart (Expt II); and 6 rows, 6.5 m long and 0.5 m apart (Expt III). Plots were always over sown and thinned at the 3-leaf stage (ligulated leaves) to the desired stand density. Nitrogen was applied twice in all experiments: at the 4-leaf stage and on *c*. 15–20 days before flowering. The application rate was always 100 kg N/ha, except for the second application in Expt II, where 50 kg N/ha was applied. Experiments were conducted under no visible water stress, and pests and weeds were adequately controlled throughout the growth cycle. Water stress was prevented by means of furrow irrigation, maintaining the soil near field capacity.

In all experiments, the PGR was increased by thinning (50% reduction in stand density) or decreased by shading (50% reduction in incident solar radiation). These treatments were performed at the following stages.

(1) Pre-flowering thinning. This treatment was used to increase the PGR from the beginning of the kernel number determination period. It was performed *c*. 10 days before 50% anthesis in Expt I, 15 days before 50% anthesis in Expt II, and *c*. 20–25 days before apical anthesis in Expt III (Pepper and Prine 1972).

(2) Flowering thinning. This treatment was used to increase the PGR at the start of the early grain-filling stage. This treatment was only done in maize experiments, and it was performed when 50% of the plants reached anthesis.

(3) Post-flowering thinning. This treatment was used to increase the PGR during the effective grain-filling period. Thinning was performed once the *lag* phase had elapsed, *c*. 15 days after 50% anthesis in maize and *c*. 10 days after apical anthesis in sorghum.

(4) Post-flowering shading. This treatment was used to decrease the PGR during the effective grain-filling period. Shade cloths (50% reduction of incident solar radiation) were placed at the end of *lag* phase, *c*. 15 days after 50% anthesis in maize and *c*. 10 days after apical anthesis in sorghum. This treatment was not performed in maize Expt II.

In each experiment, a minimum of 30 plants per replicate were tagged at random 15–25 days before flowering. Sets of 10–15 consecutive plants in the row were always used. Silking date (i.e. first silk visible) of the apical ear in maize and anthesis dates for apical and basal sections of the panicle in sorghum (after dividing the panicle into 4 equal sections on the basis of the number of whorls on the rachis; Heiniger *et al*. 1993) were registered for all tagged plants. Beginning at silking in maize and apical anthesis in sorghum, the apical ear shoot or panicle of one plant per replicate was harvested every 4 to 6 days. Sampling for kernel dry and fresh weights was done between spikelets 10 and 15 from the bottom of the apical ear in maize and from apical and basal positions within the sorghum panicle. Each individual sample always consisted of more than 10 kernels. Dry weights were determined after drying kernels in an air-forced oven at 70°C for at least 96 h. Final KW was determined for each genotype × treatment combination in maize, and for each genotype × treatment × position combination in sorghum by fitting a bilinear model (Eqns 1 and 2):

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

$$\mathrm{KW} = a + bc \text{ for } \mathrm{TT} > c \quad (2)$$

where TT is thermal time after silking or anthesis (degree-days), a is the Y-intercept (degree-days), b is kernel growth rate during the effective grain-filling period (mg/degree-day), and c is the total duration of grain filling (degree-days). The bilinear model was fitted to the kernel dry weight data of each replicate using the iterative optimisation technique of Table Curve V 3.0 (Jandel Scientific 1991). Daily TT values were obtained with a base temperature of 0°C for maize (Muchow 1990) and 5.7°C for sorghum (Heiniger *et al*. 1993). Mean daily air temperature was calculated as the average of hourly air temperatures registered at a weather station located at *c*. 50 m from experimental plots.

Non-destructive allometric models (Borrás and Otegui 2001; Vega *et al*. 2001) were used for the estimation of plant biomass at the pre- and post-flowering stages. The pre-flowering biomass sampling was done using plants removed from the pre-flowering thinning treatment. The allometric approach was used to ensure the closest representation of plant biomass corresponding to tagged plants that remained in the field until final harvest, and because we were interested in studying the individual plant level.

Allometric models were developed from 5 to 20 additional tagged plants per replicate harvested for each genotype × treatment combination. For both species, the pre-flowering model was based on the linear regression between shoot biomass per plant and the stem volume of each plant. The stem volume was calculated from plant height (from ground level up to the uppermost collar) and stem diameter at the base of the stalk. The r^2 values for this model were 0.70–0.98 ($P < 0.001$) across genotypes. The post-flowering model involved stem volume and maximum apical ear diameter for maize and stem volume and panicle height for sorghum, and it was fitted for each genotype × treatment combination using a multiple linear regression analysis. The range of r^2 values for this model was 0.70–0.82 ($P < 0.001$). The pre- and post-flowering allometric models were used to estimate the biomass of 10–15 plants per replicate that remained in the field until physiological maturity. Biomass estimation did not exceed the range of stem

volume explored by measured data. At physiological maturity (defined as 75% milk line for maize, Hunter *et al*. 1991; and when kernel moisture concentration from the basal panicle position fell below 300 g/kg for sorghum, Gambín and Borrás 2005) these plants were harvested and individual kernel number per plant determined by manual counting. Individual plant shoot biomass was always obtained after drying plants in an air-forced oven at 65°C for at least one week. Sorghum mean KW was obtained by calculating the ratio between total kernel weight per panicle and kernel number per panicle.

Plant growth rate around flowering (mg/degree-day) was calculated as the ratio between plant biomass increase (mg) from the pre-flowering to the post-flowering biomass sample, and the thermal time interval between sampling dates. Daily thermal time values for this stage were calculated using a base temperature of 8°C for maize (Ritchie and NeSmith 1991) and of 11°C for sorghum (Hammer *et al*. 1993). Plant growth rate per kernel around flowering (mg/degree-day.kernel) was obtained as the quotient between PGR during this period and the kernel number per plant counted at physiological maturity. Plant growth rate during the effective grain-filling period (mg/degree-day) was obtained as the quotient between shoot biomass increase (mg) from the post-flowering sample to physiological maturity, and the thermal time interval between these stages. Plant growth rate per kernel during the effective grain-filling period (mg/degree-day.kernel) was calculated as the ratio between PGR during this period and the number of kernels per plant.

We estimated potential kernel size by using kernel water content early in grain filling (kernel moisture concentration close to 800 g/kg for maize and close to 750 g/kg for sorghum) in apical ears and panicles of 3 plants collected from each genotype × treatment combination in all experiments. This was done following the procedures described in Borrás and Westgate (2006). Briefly, the idea was to estimate maximum water content and to use this value as a potential kernel sink estimate (Borrás *et al*. 2003). The maximum water content can be estimated from kernel water content and moisture concentration measured at any specific seed developmental stage. In order to do this for sorghum, we developed a general kernel water content growth pattern, as Borrás and Westgate (2006) did for maize. We used previously published data from an independent experiment (Gambín and Borrás 2005) to do this. A polynomial model was fitted between percent maximum water content and kernel moisture concentration for apical and basal kernels:

$$\%\mathrm{MWC} = d + e\mathrm{MC} + f\mathrm{MC}^2 + g\mathrm{MC}^3 \qquad (3)$$

where %MWC is percent of maximum water content, MC is kernel moisture concentration (percent of water content on a fresh weight basis), and d, e, f, and g are parameters of the model. The model was fitted using the iterative optimisation technique of Table Curve V 3.0 (Jandel Scientific 1991). The adjusted r^2 was 0.85. For both species, potential kernel size was estimated as the maximum water content kernels reached at mid grain filling.

For each species, differences among genotypes and treatments were determined by ANOVA as a split-plot design, with genotypes as main plots and treatments as sub-plots. In sorghum, panicle positions were treated as sub-subplots. Linear, bilinear, and nonlinear models were fitted to the variables under study. A previously used hyperbolic nonlinear model was fitted to analyse the relationship between kernel number per plant and PGR around flowering (Tollenaar *et al*. 1992; Andrade *et al*. 1999; Vega *et al*. 2001).

Results

Kernel number and plant growth rate around flowering

In maize, the pre-flowering and flowering thinning treatments increased the PGR around flowering compared with the control in all genotypes ($P < 0.001$; Table 1). There were no genotypic differences in PGR around flowering in Expt I ($P > 0.05$). The enhanced PGR around flowering increased kernel number per plant in all genotypes ($P < 0.001$; Table 1). A×888 showed a slight trend to set a higher kernel number per plant than genotype A×842 under all growth conditions ($P < 0.07$; Table 1).

For sorghum, genotypes did not differ in their PGR around flowering ($P > 0.05$; Table 2), and the pre-flowering thinning treatment enhanced the PGR around flowering similarly in all genotypes ($P < 0.001$; Table 2). Kernel number per plant was not different among genotypes at the control stand density ($P > 0.05$). The pre-flowering thinning treatment increased kernel number per plant ($P < 0.001$; Table 2), but a genotype × treatment interaction showed that not all genotypes responded similarly to the same increase in PGR ($P < 0.01$; Table 2). Kernel number per plant increased more in genotype X9946 than in DK68T (Table 2).

We further examined the kernel number per plant response to changes in PGR at the individual plant level. Examining the response of individual plants within the population rather than population averages enables us to quantify the response to a much greater range of PGRs (Vega *et al*. 2001). Tables 1 and 2 depict the average response of the plants within the canopy and the variability among these plants, while the figures describe individual plant data. When individual kernel number per plant was plotted as a function of PGR around flowering for all the measured individual plants, differences in the response pattern among genotypes within each species were evident (Fig. 2). For maize genotypes, the relationship between kernel number per plant and PGR around flowering was curvilinear in A×888 and A×842, while a linear response was evident in DK682 (Fig. 2). In sorghum, the relationship was linear for X9946, and curvilinear for X7761 and DK68T (Fig. 2).

Plant growth rate per kernel around flowering and during the effective grain-filling period

As both species showed variations in the response of kernel number per plant to PGR around flowering, depending on the genotype (Fig. 2), PGR per kernel around this period did not respond similarly across genotypes as PGR was altered (Fig. 3). Differences in PGR per kernel around flowering were detected among genotypes ($P < 0.05$) and treatments ($P < 0.001$) in maize Expt I (Table 1). As maize genotypes A×888 and A×842 showed a reduced ability to set kernels as PGR increased, PGR per kernel increased with enhanced PGR around this period (Table 1, Fig. 3). The opposite was observed for genotype DK682. The linear relationship among kernel

Table 1. For three commercial maize genotypes tested (Expts I and II), plant growth rate (PGR) around flowering (mg/degree-day, anthesis ±15 days), kernel number per plant, PGR per kernel around flowering and during the effective grain-filling period (mg/degree-day.kernel), estimated maximum water content (MWC, mg), and final kernel weight (KW, mg) at spikelet position 10–15 from the bottom of the apical ear for the control, pre-flowering thinning (anthesis –15 days), flowering thinning (anthesis), post-flowering thinning (anthesis +15 days), and post-flowering shading (from anthesis +15 days) treatments

Thinning and shading treatments consisted of reducing by 50% the stand density and the incident solar radiation, respectively. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; n.s., not significant

Treatment	PGR around flowering		Kernel number per plant		PGR per kernel				Estimated MWC[C]	KW[D]	
					Around flowering		Around effective grain-filling period				
	Mean	CV[B]	Mean	CV	Mean	CV	Mean	CV		Mean	CV
					A×888 CL-MG (Expt I)						
Control	206	16	634	14	0.33	14	0.24	21	161	290	8
Pre-flow.thinning	300	12	671	10	0.45	14	0.32	18	240	353	8
Flow.thinning	317	18	704	9	0.45	17	0.26	16	230	347	5
Post-flow.thinning	206	16	648	12	0.32	15	0.32	17		311	9
Post-flow.shading	203	15	580	14	0.34	13	0.13	30		231	14
					A×842 MG (Expt I)						
Control	218	16	596	15	0.37	13	0.22	24	267	313	8
Pre-flow.thinning	326	17	707	18	0.47	16	0.25	24	301	362	9
Flow.thinning	325	20	679	12	0.48	16	0.23	14	312	340	7
Post-flow.thinning	221	18	594	14	0.38	12	0.31	11		353	8
Post-flow.shading	210	20	519	19	0.40	14	0.16	41		278	13
Genotype (G)	**n.s.**		**n.s.**		***(0.03)**		**n.s.**		***(58)**	**n.s.**	
Treatment (T)	*****(17)[A]**		*****(42)**		*****(0.02)**		*******		****(36)**	*******	
G × T	**n.s.**		**n.s.**		**n.s.**		***(0.045)**		**n.s.**	***(24)**	
					DK682 (Expt II)						
Control	159	14	475	12	0.34	14	0.20	20	280	313	5
Pre-flow.thinning	210	13	752	25	0.29	18	0.23	24	299	320	6
Flow.thinning	193	11	702	19	0.28	17	0.24	10	243	309	6
Post-flow.thinning	155	9	509	16	0.31	16	0.26	17		308	7
Treatment (T)	*****(19)**		*****(70)**		****(0.025)**		***(0.04)**		***(35)**	**n.s.**	

[A]l.s.d. values for $P \leq 0.05$.

[B]Coefficient of variation of individual plants within the canopy (%), calculated using individual plant-to-plant data from each genotype × treatment × replicate combination.

[C]Estimated MWC was determined from the kernel water content measured *c.* 15 days after anthesis following the procedures described in Borrás and Westgate (2006). Estimated MWC for the post-flowering thinning and shading treatments is equivalent to the control.

[D]Final KW was determined by fitting a bilinear model to the kernel dry weight data of each genotype × treatment × replicate combination. Because of this, KW values from the table could not perfectly match the ones shown in Figs 4 and 5. Figures 4 and 5 show KW of individual plants.

number per plant and PGR around flowering for this genotype (Fig. 2) determined almost no response of PGR per kernel to changes in PGR around flowering (Fig. 3).

For sorghum, PGR per kernel around flowering showed a genotype × treatment interaction ($P < 0.05$, Table 2). While no changes were observed across treatments for genotype X9946, PGR per kernel around flowering was significantly increased as PGR increased for genotypes X7761 and DK68T (Table 2, Fig. 3). Recall that genotype X9946 showed a linear response of kernel number per plant to changes in PGR per kernel around the flowering period.

During the effective grain-filling period, thinning alleviated competition among plants and improved plant growth in all genotypes ($P < 0.001$), increasing the PGR per kernel during this period (Table 1). By contrast, shading treatment starting at the same developmental stage reduced PGR along this period for all treatment combinations ($P < 0.001$), decreasing the PGR per kernel during the effective grain-filling period. Plant growth rate per kernel during the effective grain-filling period did not differ among genotypes from Expt I ($P > 0.05$) but only among treatments ($P < 0.001$). DK682 showed values similar to the other genotypes (Table 1). For sorghum, PGR per kernel during the effective grain-filling period differed among genotypes ($P < 0.05$) and treatments ($P < 0.001$), and a genotype × treatment interaction was detected ($P < 0.001$; Table 2). X9946 always showed a higher PGR per kernel during the effective grain-filling period compared with the other genotypes ($P < 0.05$), even in the control environment.

It is important to note that for both species, not only the post-flowering thinning but also the pre-flowering thinning increased the PGR per kernel during the effective grain-filling period (Tables 1 and 2). Hence, increasing the plant growth from pre-flowering promoted changes in PGR per kernel during the flowering and the effective grain-filling period.

Table 2. For three commercial sorghum genotypes (Expt III), plant growth rate (PGR) around flowering (mg/degree-day, apical anthesis –20 days to apical anthesis +10 days), kernel no. per plant, PGR per kernel around flowering and during the effective grain-filling period (mg/degree-day.kernel), estimated maximum water content (MWC, mg) and final kernel weight (KW, mg) at apical (a) and basal (b) position within the panicle for the untreated control, pre-flowering thinning (apical anthesis –20 days), post-flowering thinning (apical anthesis +10 days) and post-flowering shading (from apical anthesis +10 days) treatments

Thinning and shading treatments consisted of reducing by 50% the stand density and the incident solar radiation, respectively. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; n.s., not significant

Treatment	PGR around flowering		Kernel number per plant		PGR per kernel ($10^2 \times$N)					Estimated MWC[C]	KW[D]	
					Around flowering		Around effective grain-filling period					
	Mean	CV[B]	Mean	CV	Mean	CV	Mean	CV			Mean	CV
					X9946							
Control	96	18	2801	23	3.62	17	4.08	20	a	20.2	24.4	10
									b	17.0	24.5	11
Pre-flow.thinning	137	7	3951	18	3.56	15	5.50	17	a	23.7	29.4	7
									b	19.8	28.8	7
Post-flow.thinning	93	15	2609	26	3.93	39	5.06	19	a		30.2	4
									b		30.8	5
Post-flow.shading	96	13	2731	18	3.60	17	2.15	32	a		20.5	9
									b		19.2	11
					X7761							
Control	91	21	3177	24	3.00	16	2.78	28	a	20.8	26.9	6
									b	17.6	31.6	9
Pre-flow.thinning	137	13	3859	15	3.60	11	4.17	16	a	24.3	31.0	10
									b	21.1	36.5	8
Post-flow.thinning	92	16	3144	17	2.96	14	4.56	13	a		31.3	5
									b		34.0	4
Post-flow.shading	91	24	2908	20	3.18	16	2.12	32	a		25.6	17
									b		27.5	9
					DK68T							
Control	94	11	3123	15	3.04	13	2.75	27	a	16.6	22.7	13
									b	13.9	24.5	11
Pre-flow.thinning	145	8	3430	16	4.30	14	4.42	14	a	20.0	31.1	5
									b	17.2	30.9	5
Post-flow.thinning	86	10	3071	20	2.89	19	4.67	11	a		31.3	9
									b		31.4	6
Post-flow.shading	93	11	3124	13	3.01	14	2.25	27	a		20.4	17
									b		20.9	18
Genotype (G)	**n.s.**		**n.s.**		**n.s.**		*****			*** (3.2)**	******	
Treatment (T)	***** (5.8)[A]**		*******		**n.s.**		*******			***** (0.67)**	*******	
G × T	**n.s.**		**** (294)**		*** (0.3)**		***** (0.25)**			**n.s.**	***** (1.5)**	
Position (P)										***** (0.67)**	*******	
G × P										**n.s.**	***** (1)**	
G × T × P										**n.s.**	**n.s.**	

[A]l.s.d. values for $P \leq 0.05$.

[B]Coefficient of variation of individual plants within the canopy (%), calculated using individual plant-to-plant data from each genotype × treatment × replicate combination.

[C]Estimated MWC was determined from the kernel water content measured *c*. 10 days after anthesis at each position following the procedures described in Borrás and Westgate (2006) for maize. Estimated MWC for the post-flowering thinning and post-flowering shading treatments is equivalent to the control.

[D]Final KW was determined by fitting a bilineal model to the kernel dry weight data of each genotype × treatment x position × replicate combination. Because of this, KW values from the table could not perfectly match the ones shown in Figs 4 and 5. Figures 4 and 5 show KW of individual plants.

Final kernel size

Treatments modified maize KW at maturity in Expt I ($P < 0.001$; Table 1), but there were not differences among treatments in Expt II ($P > 0.05$). A genotype × treatment interaction was detected in Expt I ($P < 0.05$; Table 1), mainly because the post-flowering thinning only increased KW in one of the genotypes (A×842). The shading treatment reduced KW by *c*. 20% in both genotypes compared with the control, and the pre-flowering and the flowering treatments increased KW by 10–20% compared with the control (Table 1).

Sorghum genotypes showed significant differences in their KW at maturity ($P < 0.01$) and treatments modified KW differently depending on the genotype ($P < 0.001$; Table 2). Shading treatments during the effective grain-filling period always reduced KW *c*. 10–20% compared with the control (Table 2). Thinning the crop to enhance total plant growth increased KW to similar levels independently of the timing of

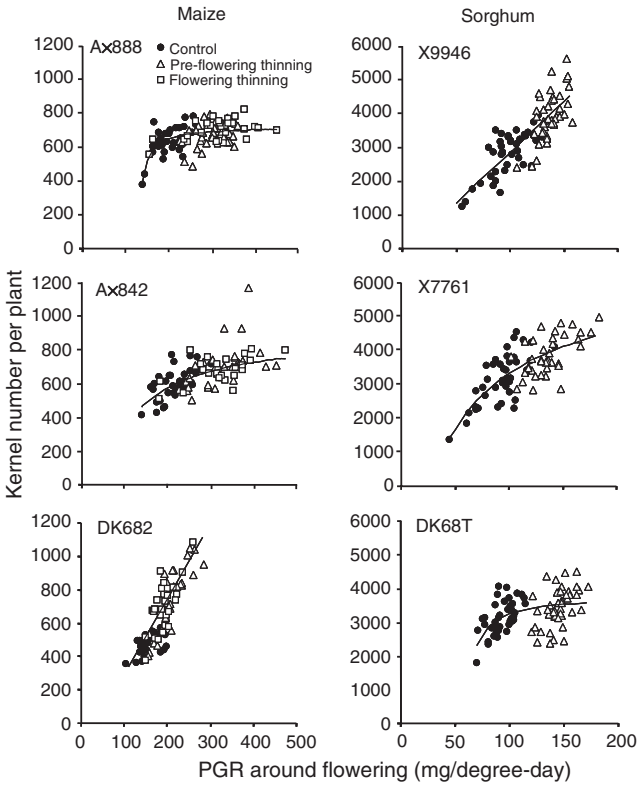

Fig. 2. Relantionship between kernel number per plant and plant growth rate (PGR) around flowering for maize genotypes A×888 CL-MG (Expt I), A×842 MG (Expt I) and DK682 (Expt II), and for sorghum genotypes X9946, X7761 and DK68T (Expt III). Treatments are represented as: closed symbols, control; open triangles, pre-flowering thinning (from anthesis –15 days for maize and apical anthesis –20 days for sorghum); open squares, flowering thinning. Thinning treatments reduced the stand density by 50%. Fitted models: kernel number per plant = [89.7 * (PGR – 129)]/[1 + 0.12 * (PGR – 129)], (aj. $r^2 = 0.34$; $P < 0.001$) for A×888; kernel number per plant = [10.5 * (PGR – 50.17)]/[1 + 0.011 * (PGR – 50.17)], (aj. $r^2 = 0.45$; $P < 0.001$) for A×842; kernel number per plant = –194.8 + 4.47 * PGR, (aj. $r^2 = 0.68$; $P < 0.001$) for DK682; kernel number per plant = –173 + 30 * PGR, (aj. $r^2 = 0.66$; $P < 0.001$) for X9946; kernel number per plant = [92.15 * (PGR – 25)]/[1 + 0.014 * (PGR – 25)], (aj. $r^2 = 0.54$; $P < 0.001$) for X7761; kernel number per plant = [563.7 * (PGR – 59)]/[1 + 0.15 * (PGR – 59)], (aj. $r^2 = 0.20$; $P < 0.001$) for DK68T.

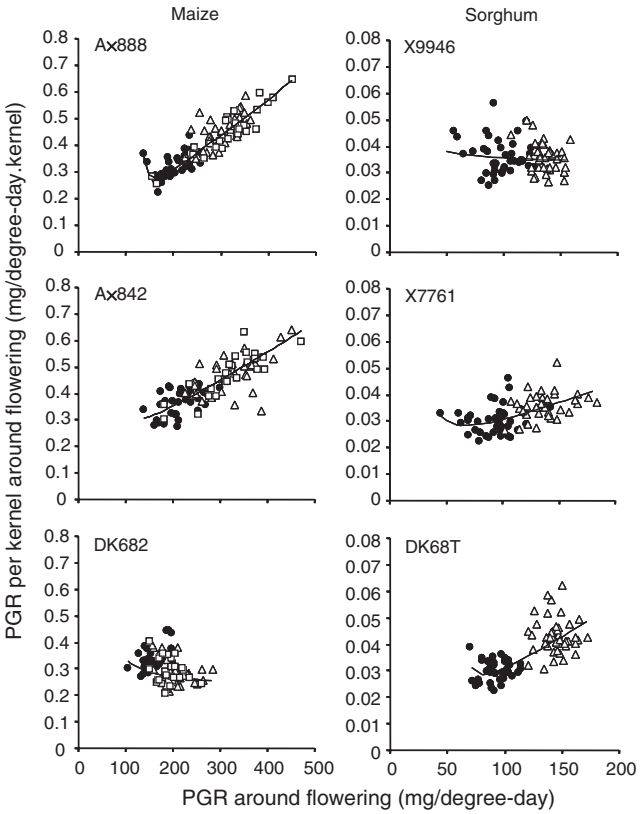

Fig. 3. Plant growth rate (PGR) per kernel as a function of PGR, both around flowering for maize genotypes A×888 CL-MG (Expt I), A×842 MG (Expt I) and DK682 (Expt II) and sorghum genotypes X9946, X7761, and DK68T (Expt III). Symbols as in Fig. 2. For each genotype, the line depicts the calculated inverse from the model fitted in Fig. 2.

the treatment (i.e. at pre- or post-flowering). When KW from different positions within the panicle was considered, KW showed a genotype × panicle position interaction ($P < 0.001$). Genotype X7761 showed a consistently higher KW at the basal panicle position across treatments, while no differences between positions were detected for genotypes X9946 and DK68T (Table 2).

We further analysed these KW differences taking into consideration the PGR per kernel at different developmental stages (Fig. 1). As hypothesised (Fig. 1*c*), there was a positive correlation between final KW and PGR per kernel around flowering for maize genotypes A×888 and A×842 (Fig. 4). Because PGR per kernel around flowering remained almost unchanged as PGR around flowering increased in genotype DK682 (Fig. 3), no relationship was found between final KW and PGR around flowering for this genotype (Fig. 4). As such, variation in PGR around flowering affected the number of kernels set per plant, and the relationship between plant growth and kernel set helped to explain differences in maize KW in the 3 evaluated genotypes.

For maize, the average kernel size for all the plants within each canopy was also positively related to the amount of assimilates available per growing kernel during the effective grain-filling period in genotypes A×888 and A×842, and not in DK682 (Table 1). When individual plants were considered, there was a positive relationship with plateau between final KW and PGR per kernel during the effective grain-filling period for A×888 and A×842 (Fig. 5). As hypothesised (Fig. 1*d*), KW decreased compared with the control when plants were shaded during this period (Fig. 5). But increasing the assimilate availability per kernel only during the effective grain-filling period did not increase KW (Fig. 5). When the average KW from all plants within the canopy was considered, a significant KW increase was detected in only one genotype (A×842) at the post-flowering thinning treatment. This increase, however, was only *c*. 13% compared with the control.

For sorghum, KW increased when thinning at pre-anthesis significantly increased PGR per kernel at flowering (Table 2, Fig. 4). However, KW appeared to be tightly linked to the PGR

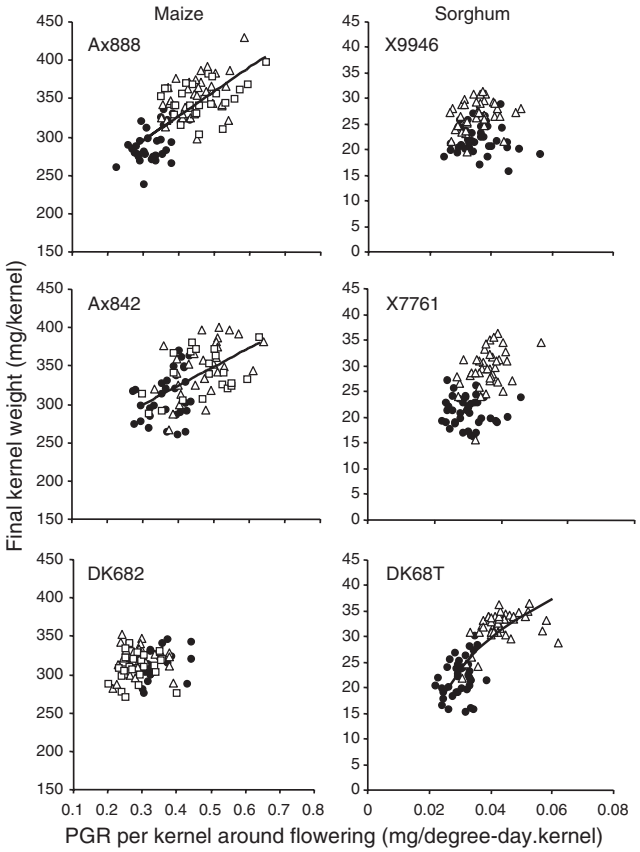

Fig. 4. For the period around flowering, relationship between final kernel weight (KW) and plant growth rate (PGR) per kernel for maize genotypes A×888 CL-MG (Expt I), A×842 MG (Expt I) and DK682 (Expt II) and sorghum genotypes X9946, X7761 and DK68T (Expt III). Symbols as in Fig. 2. Sorghum kernel weight is the mean individual kernel weight of the panicle. Fitted models: KW = 198 + 319 * PGR per kernel (aj. $r^2 = 0.52$; $P < 0.001$) for A×888; KW = 224 + 245 * PGR per kernel (aj. $r^2 = 0.30$; $P < 0.001$) for A×842; KW = [2257 * (PGR per kernel − 0.012)]/[1 + 40 * (PGR per kernel − 0.012)], (aj. $r^2 = 0.61$; $P < 0.001$) for DK68T. No significant correlation was found for the other genotypes.

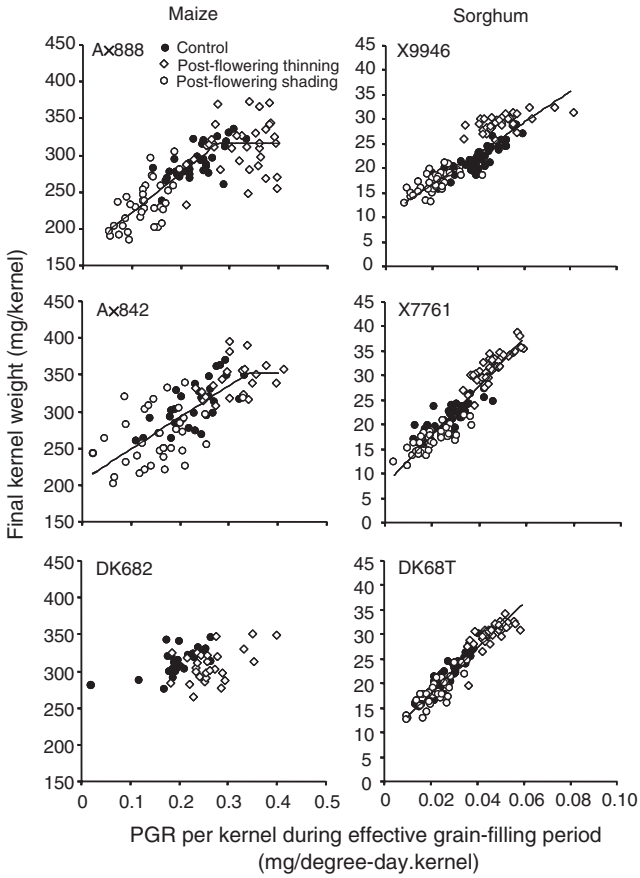

Fig. 5. For the effective grain-filling period, final kernel weight (KW) and plant growth rate (PGR) per kernel for maize genotypes A×888 CL-MG (Expt I), A×842 MG (Expt I) and DK682 (Expt II) and sorghum genotypes X9946, X7761 and DK68T (Expt III). Treatments are represented as: closed symbols, control; open rhombus, post-flowering thinning (from anthesis +15 days for maize and apical anthesis +10 days for sorghum); open circles, post-flowering shading (from anthesis +15 days for maize and apical anthesis +10 days for sorghum). Sorghum kernel weight is the mean individual kernel weight of the panicle. Fitted models: KW = 166 + 536 * PGR per kernel^(PGR per kernel ≤ 0.27) + 144.72^(PGR per kernel > 0.27), (aj. $r^2 = 0.66$; $P < 0.001$) for A×888; KW = 205 + 430 * PGR per kernel^(PGR per kernel ≤ 0.33) + 141.9^(PGR per kernel > 0.33), (aj. $r^2 = 0.55$; $P < 0.001$) for A×842; KW = 10.26 + 317 * PGR per kernel (aj. $r^2 = 0.78$; $P < 0.001$) for X9946; KW = 7.46 + 504 * PGR per kernel (aj. $r^2 = 0.88$; $P < 0.001$) for X7761; KW = 8.51 + 464 * PGR per kernel (aj. $r^2 = 0.91$; $P < 0.001$) for DK68T. No significant correlation was found for the other genotypes.

per kernel during the effective grain-filling period (Fig. 5). Kernel weight at maturity increased in all genotypes when PGR per kernel was increased only during the effective grain-filling period. This increase was *c.* 24% in X9946, 18% in X7761, and 36% in DK68T compared with the control. As such, sorghum KW always consistently increased when plant growth was increased during advanced stages of kernel development. As hypothesised (Fig. 1*h*), decreased PGR per kernel during the effective grain-filling period reduced final KW compared with the control (Table 2).

Potential kernel size

We have hypothesised that increasing PGR per kernel around flowering would increase KW through changes in the potential kernel size. To test this, we estimated the potential kernel maximum water content, an easy measurement to estimate potential kernel size. This was done by measuring kernel water content at the end of the *lag* phase.

Estimated maize maximum water content differed between genotypes ($P < 0.05$) and treatments in Expt I ($P < 0.01$) and Expt II ($P < 0.05$; Table 1). These differences in estimated maximum water content were consistent with changes in PGR per kernel around flowering (Fig. 6*a*, Table 1). The genotype that showed no variations in PGR per kernel around flowering (DK682) showed no differences in the potential kernel size established at the end of the *lag* phase, while the 2 genotypes that showed changes in PGR per kernel around flowering also showed changes in the potential kernel size. For sorghum, estimated maximum water content differed across genotypes ($P < 0.05$), treatments ($P < 0.001$) and panicle positions

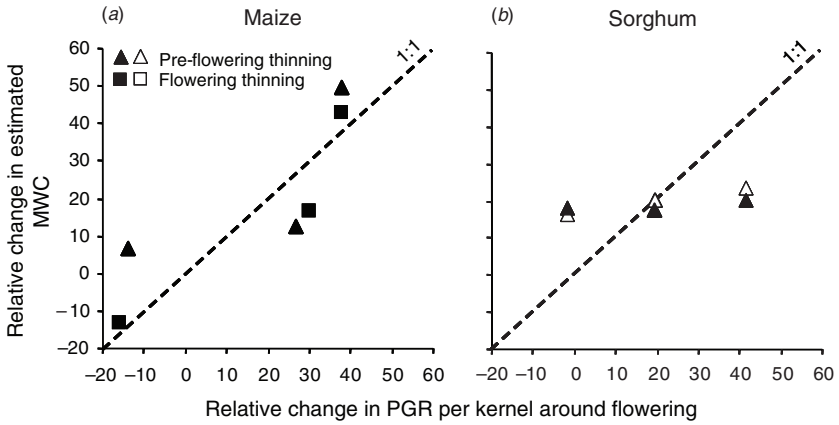

Fig. 6. Relationship between the relative change in estimated maximum water content (MWC) and the relative change in plant growth rate (PGR) per kernel around flowering for (*a*) the 3 maize and (*b*) sorghum genotypes tested. Different genotypes are represented with the same symbol for clarity. Treatments are represented as: triangles, pre-flowering thinning (from anthesis –15 days for maize and apical anthesis –20 days for sorghum); squares, flowering thinning. In *b*, closed symbols represent apical kernels and open symbols represent basal kernels. Values (average value from Tables 1 and 2) are relative to the control for each particular genotype. Thinning treatment reduced the stand density by 50%.

($P < 0.001$; Table 2). These differences, however, were not always explained by changes in the PGR per kernel around flowering (Fig. 6*b*, Table 2).

Discussion

As hypothesised, the relationship between kernel number per plant and PGR was important for explaining final kernel size in both species, maize and sorghum. The response of kernel number per plant to changes in PGR around flowering was more variable than expected. In Fig. 1 we described a curvilinear relationship for maize and a linear one for sorghum, but our data showed that both species can respond with linear and curvilinear patterns depending on the specific genotype (Fig. 2). Several studies have reported that the response of kernel number to resource availability per plant around flowering can be linear or curvilinear depending on the genotype and the particular range of PGR explored (Tollenaar *et al*. 1992; Kiniry and Knievel 1995).

In maize, changes in PGR per kernel at flowering were correlated with changes in potential and final kernel size, while in sorghum this was not evident (Fig. 6). These results are in agreement with previous maize studies showing the importance of assimilate availability per kernel at early kernel developmental stages for defining final kernel size (Borrás and Westgate 2006; Gambín *et al*. 2006). A positive correlation between final KW and PGR per kernel during the effective grain-filling period can be found in 2 genotypes when considering thinning treatments performed at pre- and post-flowering stages (Table 1). This positive correlation can be also depicted when considering individual control plants (Fig. 5). These correlations, however, were a consequence of improved growth conditions that started at earlier stages, as thinning at post-flowering did not increased final KW (Fig. 5). These results have important implications for understanding previous studies correlating KW and plant growth per kernel during effective grain filling (Maddonni *et al*. 1998, 2006; Borrás and Otegui 2001), because the relationship might not be causal. When studying sorghum source–sink yield limitations, Fischer and Wilson (1975) stated that there is a need to alter one of the processes independently of the other because sources and sinks vary non-independently throughout the growing season. When manipulative treatments were used to alter the maize source–sink ratio during grain filling, an almost null KW increase was found when assimilate availability per kernel was enhanced only during the effective grain-filling period (Schoper *et al*. 1982; Jones and Simmons 1983; Andrade and Ferreiro 1996). Hence, at the start of the effective grain-filling period maize plants set a total potential sink capacity (kernel number and individual kernel size) that places further kernel growth close to saturated assimilate availability conditions (Borrás *et al*. 2004). Maize KW will increase only if the potential size defined during the *lag* phase is increased.

Our results showed that final KW decreased in a similar fashion in both species when assimilate availability per kernel was reduced during the effective grain-filling period (Fig. 5). Our previous quantitative analysis suggested maize kernel size to be more responsive than sorghum to source reductions, but an important degree of variation in the reduction in KW was observed for a similar reduction in assimilate availability per kernel (Borrás *et al*. 2004; Gambín and Borrás 2007). Our current approach using PGR per kernel during the effective grain-filling period estimated the assimilate availability amount produced per kernel per unit of thermal time, which helps increase the accuracy of the actual source–sink ratio. By doing so, we showed that the same kind of manipulation (50% reduction in solar radiation) reduced PGR per kernel during the effective grain-filling period (and final weight) differently across genotypes (Tables 1and 2). Hence, conclusions about susceptibility under source-limited conditions given only on the basis of the performed manipulation

treatment with no data describing the actual change in source availability per growing sink (Echarte *et al*. 2006) should be made with care, as treatments might not affect genotypes similarly.

Sorghum KW increased whenever PGR per kernel was enhanced (Fig. 5). This is in agreement with our hypothetical framework based on previous studies showing that sorghum kernels normally grow below the source conditions that allow kernels to reach their potential size (Fischer and Wilson 1975; Muchow and Wilson 1976; Kiniry 1988; Gambín and Borrás 2007). Also, changes in potential kernel size in sorghum were not correlated with changes in PGR per kernel around flowering (Fig. 6*b*). It is important to understand that our current framework is based on total plant growth per established sink, and not on biomass allocation to the reproductive structure where kernels are set. Potential kernel size might be a consequence of biomass allocation to the reproductive tissue per established sink. This could be a better estimate of assimilate availability reaching each established sink compared with the total plant growth per kernel. Hence, future studies will need to evaluate this framework with detailed measurements of biomass partitioning to the reproductive structures around the kernel set period in both species.

Sadras (2007) hypothesised that crop species with low plasticity in kernel number would show more variability in grain size than species with more plasticity, while crop species showing a high plasticity in kernel number would normally have a relatively low variability in grain size. In his approach, high/low plasticity in kernel number is a consequence of the kernel number response to changes in PGR around flowering. Our analysis examining the dynamic relationships between PGR around flowering, kernel set, and potential kernel size using PGR per kernel as an estimate of the assimilate availability per kernel early in grain filling helps the study of this kernel number *v.* size interaction not only across species but also across genotypes.

Conclusions

Results were in agreement with our working hypothesis, where the response pattern of kernel number per plant to PGR modifications around flowering was critical for understanding final kernel size for a species that is predominantly sink-limited during the effective grain-filling period, such as maize. By contrast, for a species such as sorghum that shows kernel size to be highly responsive to source availability per kernel during the entire grain-filling period, the PGR per kernel during the effective grain-filling period was critical.

Our simple approach using PGR per kernel to estimate assimilate availability per kernel at different crop developmental stages was sensitive enough to capture not only species but genotype differences in their individual kernel size determination pattern. It was also useful for studying KW determination at the canopy and individual plant levels.

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