

Yield components of maize as affected by short shading periods and thinning

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Abstract. Maize (*Zea mays*) grain yield has been described to be particularly susceptible to environmental conditions around silking; however, a better temporal description of the effect of resource deprivation during this period is needed. Additionally, yield progress and the subsequent increase in the demand of assimilates may result in source limitation during the grain-filling period in current hybrids. This work assessed the effect of (i) short (~5 days) and intense shading stresses imposed at different times, and (ii) thinning during the effective grain-filling period, on yield components of an Argentinean, widespread hybrid. Grain yield was affected by resource availability during an extended period from ~300 growing degree-days (GDD) before silking to ~780 GDD after silking (base temperature = 8°C). Kernel number (KN) was reduced by shading treatments imposed within a relatively extended period of ~700 GDD centred on silking. Within this period, we establish a critical period of ~30 days around silking (i.e. –200 to 250 GDD after silking), in which KN susceptibility was maximal. The variation in KN during this period of 450 GDD was mainly accounted for by resource availability and not by timing of treatment imposition within this window. A direct relationship between KN and weight per kernel (KW) for shading treatments imposed from 0 to 200 GDD after silking indicated that compensation of KN reduction by KW increase might not be expected when stress occurred immediately after silking. Kernel number and KW presented an inverse relationship when shading took place after 200 GDD after silking. In addition, thinning after the onset of the effective grain-filling period increased KW. The results indicate that, even in the undisturbed crop, KW was limited by source capacity during grain filling. It is suggested that there is a need to reconsider current agronomic practices and breeding strategies, focusing on the source capacity during the grain-filling period.

Additional keywords: ear demand, kernel number, kernel weight, shade, sink, stress, thinning.

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Introduction

Maize grain yield results from the combination of kernel number (KN) per unit area and weight per kernel (KW). Kernel number is strongly associated with grain yield, whereas KW is considered a more stable trait (Cirilo and Andrade 1994; Otegui 1995). Kernel number is particularly susceptible to environmental conditions close to silking (Kiniry and Ritchie 1985; Westgate and Boyer 1986; Tollenaar *et al.* 1992; Andrade *et al.* 1999). Moreover, potential KW is established early during grain development (Jones *et al.* 1996). There have been many investigations of the effect of stress imposition close to silking on maize yield components; however, the period of maximum responsiveness is not clear. For instance, some authors concluded that the period centred on flowering is critical for kernel set (Claassen and Shaw 1970; Hall *et al.* 1981; Fischer and Palmer 1984), whereas others concluded that the period of ear elongation (Otegui and Bonhomme 1998) or the near post-anthesis period (Kiniry and Ritchie 1985; Grant *et al.* 1989) is the most critical. It also remains unclear whether the response of KW to stress imposition during the early stages of grain filling is negative or

positive (Ouattar *et al.* 1987; Jones *et al.* 1996; Gambín *et al.* 2006). Only a few studies have attempted to quantify and describe the effect of timing of resource deprivation on yield components around silking (Claassen and Shaw 1970; Hall *et al.* 1981; Fischer and Palmer 1984; Kiniry and Ritchie 1985; Grant *et al.* 1989; Jia *et al.* 2011). In these studies, however, plants were stressed for relatively long periods, preventing a more precise description of the effect of timing of stress on yield components. An analysis with increased temporal resolution is necessary to improve the understanding of the effect of timing of resource deprivation on yield components.

Maize (*Zea mays* L.) potential yield has been increasing during recent decades. For instance, yield has been reported to have increased at a rate of 132–166 kg ha⁻¹ year⁻¹ in Argentina (Echarte *et al.* 2000; Luque *et al.* 2006) and 74 kg ha⁻¹ year⁻¹ in the USA (Duvick 1997). Yield progress has been mainly accounted for by an increase in KN per unit area (Luque *et al.* 2006). The indicated increase in KN resulted in increased demand for assimilates during the grain-filling period (Echarte *et al.* 2006), which could lead to a source-limiting condition.

Hence, it is relevant to investigate the effect of resource availability during the grain-filling period on yield components of current maize hybrids.

Knowledge about yield component determination and the degree of source limitation during grain filling will be relevant for the design of agronomic practices (i.e. irrigation scheduling, fertilisation routine, and pest and disease management) and to understand the effect of adverse climate on yield. This information should also guide future breeding strategies (Tollenaar and Lee 2011).

The objectives of this work were to assess the effects of (i) short and intense shading stresses imposed at different times during the crop cycle, and (ii) thinning during the effective grain-filling period, on yield components of a current maize hybrid. The results of this work will allow accurate analysis of the effect of resource deprivation on KN and establish the degree of source limitation during the grain-filling period.

Materials and methods

Experimental design and crop management

Three experiments were carried out at the INTA-Balcarce experimental field, Buenos Aires, Argentina (37.5°S, 58.2°W) during the 2009–10 (Expt 1), 2010–11 (Expt 2), and 2011–12 (Expt 3) growing seasons. Experiments were established on a Typic Argiudol (USDA Taxonomy; Soil Survey Staff 2010) with an effective depth of 1.5 m and 5.6% topsoil organic matter content. The maize hybrid used in the experiments was DK 747 MGRR2 (relative maturity 124; Monsanto Company (Argentina), Buenos Aires). This currently widespread hybrid, released in 2007, presents high yield potential (i.e. average 14 t grain ha⁻¹ on a dry weight basis in the present experiments). Experiments were sown on 20 October (Expt 1 and Expt 2) and 6 October (Expt 3). Plots were oversown in rows spaced at 0.7 m with hand planters and were thinned at the V2 stage (Ritchie and Hanway 1982) to a uniform density. Plant density was 7.2 plants m⁻² in Expt 1. Plant density was increased to

8.8 plants m⁻² in Expt 2 and 8.5 plants m⁻² in Expt 3 in order to increase the stress per plant. Experimental area consisted of 20 rows of 40 m length.

Based on soil analysis and in order to provide adequate mineral nutrition, experiments were fertilised with 40 kg ha⁻¹ of phosphorus (P) incorporated into the soil before sowing and with 300 kg nitrogen (N) ha⁻¹ and 40 kg sulfur (S) ha⁻¹ incorporated by irrigation, half at the V5 stage and the other half at the V15 stage. Soil water content was kept at >65% of field capacity by complementing rainfall with sprinkler irrigation. Weeds were chemically and manually controlled. Commercial triazole fungicide was applied at the V10 stage to prevent fungal diseases.

Treatments consisted of short shading periods (5.4 days average) imposed at different times across the crop cycle (Table 1), thinning imposed at the end of R4 stage, and an untreated control. Expt 1 evaluated 19 different shading timings and a control (i.e. Expt 1: 20 treatments). Expt 2 evaluated 15 different shading timings, thinning at the end of R4 stage, and a control (i.e. Expt 2: 17 treatments). Expt 3 evaluated four different shading timings, thinning at the end of R4 stage, and a control. In addition, Expt 3 evaluated two shading intensities for the first three shading timings (i.e. Expt 3: nine treatments).

The reduction in incoming photosynthetically active radiation (PAR) during shading treatment imposition, as determined by measurements in the field, was 74% in Expt 1 and 86% in Expt 2. The levels of reduction in incoming PAR evaluated in Expt 3 were: (i) 86% for all shading timings, and (ii) 65% for the first three shading timings only. These differences in the reduction of incoming radiation among experiments were designed to explore the effect of the level of stress. Shading treatments were achieved with tents made with steel frames 1.4 m wide and 2.3 m long, upon which shade cloth was mounted. Thinning treatment consisted of removing alternately half of the plants of four rows along 4.6 m. Shading and thinning were performed in two blocks (replications) in all experiments, and at least five

Table 1. Central time of shading imposition expressed as days after silking (DAS) and growing degree-days after silking (GDDAS), length of shading period (LST) expressed in growing degree-days, and incident photosynthetically active radiation (PAR) during treatment imposition for Experiments 1, 2, and 3

Phenology: Stage:	Vegetative			Reproductive																	
	V6	V7	V8	V10	V12	V14	V17	R1	R2	R3	R4	R5									
<i>Expt 1</i>																					
DAS	-38	-33	-28	-23	-18	-10	-5	-1	4	9	14	19	23	28	32	38	45	52	60		
GDDAS	-469	-426	-374	-312	-244	-147	-67	-11	50	123	201	289	356	425	483	547	617	699	794		
LST (GDD)	32	55	55	68	67	74	55	64	72	58	84	83	65	69	64	86	55	91	72		
PAR (MJ m ⁻²)	47	40	51	36	42	101	103	116	104	93	110	96	76	113	94	146	118	90	127		
<i>Expt 2</i>																					
DAS			-27	-20		-14		-6	1	8	15	21	27	36		41		57	65	71	78
GDDAS			-410	-298		-201		-88	10	105	213	283	343	467		527		672	761	837	890
LST (GDD)			80	81		107		69	74	83	72	66	69	79		59		96	55	63	61
PAR (MJ m ⁻²)			155	122		150		119	138	129	140	129	135	91		98		98	67	99	109
<i>Expt 3</i>																					
DAS									5	13		20				42					
GDDAS									90	209		328				645					
LST (GDD)									86	73		81				81					
PAR (MJ m ⁻²)									141	129		98				117					

untreated control plots were established along each block (i.e. five in Expt 1, eight in Expt 2, and five in Expt 3). A minimum distance of 1.2 m was kept among experimental units.

Ears from each experimental unit were harvested after physiological maturity, from the central 6, 10, and 12 plants for Expts 1, 2, and 3, respectively. Ears were hand-threshed; kernels per ear were counted and weighed after they were dried to constant weight at 90°C to estimate KN, KW, and grain yield.

Daily mean temperature and daily incident PAR were recorded at a weather station 800 m from the experimental site. Daily growing degree-day (GDD) values were calculated using daily mean temperature derived from the weather station data and a base temperature of 8°C. The effect of shading treatment on canopy temperature was evaluated by comparing temperature measured at the canopy level inside and outside the tents during at least one entire day. Average daily incoming PAR on a per-plant basis was derived for different periods within the time window in which KN was significantly affected by treatments.

Data analyses

Data were analysed as a completely randomised block design with two replications. Analysis of variance was performed for each experiment using the R Commander package (R Software; De Mendiburu 2009). Dunnett's procedure (Steel and Tome 1960) was performed to test for differences from the control at $P=0.05$ (Kiniry and Ritchie 1985) using the R Agricolae package (R Software; De Mendiburu 2009). In addition, data were processed by linear regression analysis using GraphPad Prism 5 software (Motulsky and Christopoulos 2003). Data were expressed as a percentage of the control plots mean for each experiment, when necessary.

Results

Growing conditions and development

Timing and duration of shading for all treatments and incident radiation during treatment imposition are summarised in Table 1. Treatments (even those imposed before silking) did not affect time to silking compared with the controls; this is consistent with the reduced effect of shading on daily mean canopy temperature, which was <0.5°C. Silking occurred 770 GDD (70 days), 830 GDD (72 days), and 788 GDD (77 days) after emergence for Expts 1, 2, and 3, respectively. Physiological maturity for control plots occurred at 840 (66 days), 863 (67 days), and 954 GDD (66 days) after silking for Expts 1, 2, and 3, respectively.

Grain yield

Grain yield for the control treatments expressed on a dry weight basis was 1346.4, 1402.5, and 1453.5 g m⁻² for Expts 1, 2, and 3, respectively. Expressed as yield per plant, these values were 187, 165, and 171 g plant⁻¹. Grain yield variation for control plots within each experiment was low (CV% 4.1, 3.9, and 4.5 for Expts 1, 2, and 3, respectively). Shading treatments reduced grain yield when imposed from ~300 GDD before to 780 GDD after silking (Fig. 1, Expts 1 and 2). Accordingly, the seven shading treatments imposed in Expt 3, which were included in that time-frame, also reduced yield (Table 2). On the other hand, thinning during the effective grain-filling stage

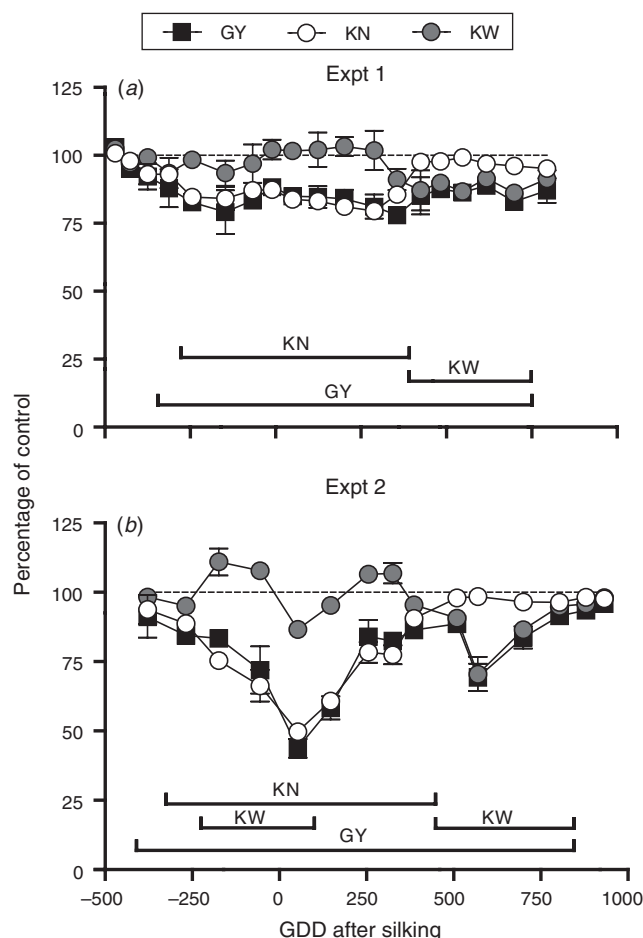


Fig. 1. Grain yield (GY), kernel number (KN), and weight per kernel (KW) expressed as a percentage of the control (dashed line) as a function of the time of shading imposition expressed in growing degree-days (GDD) after silking for (a) Expt 1 and (b) Expt 2. Shading reduced incident radiation by 65% in Expt 1 and 85% in Expt 2. Each point represents the mean of two replications. Horizontal brackets enclose the periods where GY, KN, or KW were different from the control (Dunnett test, $\alpha=0.05$). Capped vertical bars represent \pm s.e. and are not shown when smaller than the symbol size.

increased yield per plant by 15% and 9% relative to the control in Expt 2 and Expt 3, respectively (Table 3). Yield variation was mainly accounted for by KN for treatments imposed until ~400 GDD after silking ($R^2=0.86$) and by KW afterward ($R^2=0.91$; Fig. 1).

Kernel number

Kernel number per plant for the control treatment averaged 602, 579, and 570 for Expts 1, 2, and 3, respectively. Shading treatments imposed during a period of ~700 GDD around silking reduced KN relative to the control treatment (Fig. 1). The effect of the treatments was similar during all of this period in Expt 1, averaging a 17% reduction. Nevertheless, shading imposed closely around flowering in Expt 2 resulted in the highest reduction in KN (Fig. 1). In Expt 3, KN was also reduced compared with the control by shading treatments

imposed within this window of 700 GDD (i.e. first three timings), and this reduction was consistently greater for the 85% shading intensity than for the 65% shading intensity.

Kernel number was reduced from around -300 to 400 GDD after silking. The effect of timing and intensity of resource deprivation on KN was further analysed within this interval using the pooled data from all experiments and relating KN to incoming PAR per plant. This last variable integrates the effect of plant density (7.2, 8.8, and 8.5 plants m⁻² for Expts 1, 2, and 3,

respectively), shading timing, shading intensity, and year. A strong and positive relationship was found between KN and averaged daily incoming PAR per plant from 200 GDD before silking to 250 GDD after silking, i.e. a period of ~30 days around silking that includes the critical period for grain setting proposed by other authors (Hall *et al.* 1981; Kiniry and Ritchie 1985; Otegui and Bonhomme 1998). The relationship was: $KN = 631.6 (1 - \exp(-5.874 (\text{PAR plant}^{-1} - 0.94)))$; $R^2 = 0.90$ (Fig. 2a). The accuracy of this relationship indicates that resource availability rather than

Table 2. Kernel number, weight per kernel, and grain yield relative to the control for four different times of shading imposition, expressed in growing degree-days after silking (GDDAS), and two shading intensities (65 and 85%) for Experiment 3

Values are mean percentages ± standard deviation. * $P < 0.05$ for difference from the control

GDDAS	Kernel number		Kernel weight		Grain yield	
	Shading intensity		Shading intensity		Shading intensity	
	85%	65%	85%	65%	85%	65%
90	61.1 ± 9.0*	79.0 ± 8.6*	87.8 ± 0.9*	98.1 ± 2.8	78.8 ± 25.4*	77.5 ± 12.0*
209	78.8 ± 2.2*	87.6 ± 0.7*	97.1 ± 9.4	102.0 ± 3.6	84.0 ± 20.0*	89.4 ± 3.9*
328	62.1 ± 10.5*	75.8 ± 8.9*	101.4 ± 3.1	105.9 ± 0.2	72.8 ± 26.1*	80.3 ± 9.8*
645	95.5 ± 2.7		88.3 ± 2.8*		92.5 ± 16.5*	

Table 3. Kernel number per plant and weight per kernel for thinning and control treatment in Experiments 2 and 3
For the thinning treatment, both variables are also expressed as a percentage of the control. ** $P < 0.01$ for difference from the control

		Kernel number		Kernel weight	
		(no. plant ⁻¹)	(% of control)	(mg kernel ⁻¹)	(% of control)
Expt 2	Control	579		283	
	Thinning	578	99.8	326**	115
Expt 3	Control	570		301	
	Thinning	582	101.4	328**	109

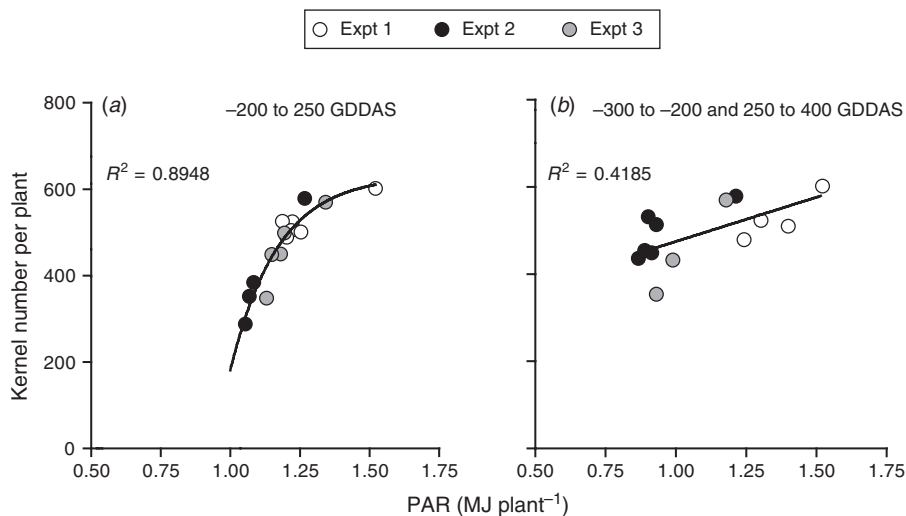


Fig. 2. Kernel number per plant (KN) as a function of average daily incoming photosynthetically active radiation (PAR) per plant for two different periods: (a) -200 to 250 and (b) -300 to -200 plus 250 to 400 growing degree-days (GDD) after silking. Data were collected from all three experiments (Expts 1, 2, and 3). Each point represents the mean of two replications. Fitted functions: (a) $KN = 631.6 (1 - \exp(-5.874 (\text{PAR plant}^{-1} - 0.94)))$ and (b) $KN = 203 \text{ PAR plant}^{-1} + 271.8$ ($P = 0.0169$).

the timing of treatment imposition was the major factor controlling kernel number during the period of 450 GDD around silking. By contrast, the relationship between KN and resource availability was weak when considering the period before and after the indicated window of 450 GDD (i.e. from -300 to -200 plus from 250 to 400 GDD after silking; Fig. 2*b*).

Kernel number was not affected when shading was imposed beyond 400 GDD after silking for Expt 1 and Expt 2 (Fig. 1), which occurred shortly after the beginning of milk stage (R3: 300 GDD after silking; Table 1). In accordance, in Expt 3, KN was not affected by the only shading treatment imposed during advanced effective grain filling (645 GDD after silking; Table 2). Finally, thinning (Expt 2 and Expt 3) did not affect KN (Table 3).

Kernel weight

Weight per kernel for the control treatment was 311, 283, and 301 mg in Expts 1, 2, and 3, respectively. Weight per kernel was reduced by shading imposed during the grain-filling period, i.e. from 425 to 699 GDD after silking in Expt 1 and from 479 to 773 GDD after flowering in Expt 2 (Fig. 1), and at 645 GDD after silking in Expt 3 (Table 2). By contrast, thinning during the effective grain-filling period (Expt 2 and Expt 3) increased KW compared with the control (Table 3).

Shading treatment imposition around silking also altered KW relative to the control. The responses, however, were not consistent. Shading before silking increased KW in Expt 2 and never resulted in KW reductions. Furthermore, shading immediately after silking reduced KW only when resource availability per plant was low (i.e. in Expt 2 and Expt 3, in which plant density and shading intensity were high; Fig. 1,

Table 2). Despite the apparent lack of consistency in the response of KW to treatment imposition immediately after silking, KW and KN were strongly and positively associated when data were pooled from all experiments for shading imposed from 0 to 200 GDD after silking ($KW = 0.42 KN + 66$; $R^2 = 0.61$, $P < 0.001$; Fig. 3*a*). By contrast, a strong inverse association between the two yield components was observed when data were pooled from shading treatments imposed from 200 to 780 GDD after silking ($KW = -0.65 KN + 151$; $R^2 = 0.53$, $P < 0.001$; Fig. 3*b*).

Discussion

Yield components

Kernel number

The high susceptibility of KN to resource deprivation close to flowering has been extensively documented for maize. Nevertheless, there is some discussion about which specific period is more critical for kernel set. Some authors concluded that the period centred on flowering is the most critical for kernel set (Claassen and Shaw 1970; Hall *et al.* 1981; Fischer and Palmer 1984), others speculated that the period in which the ear elongates is the most critical (from -227 to +100 GDD after silking; Otegui and Bonhomme 1998), whereas others concluded that the near post-anthesis period is the most critical (Kiniry and Ritchie 1985; Grant *et al.* 1989). Our study contributed to clarifying these discrepancies by studying the response of KN to resource deprivation with an increased temporal resolution.

Kernel number was reduced by short periods of resource deprivation along a wide time-frame that extended from ~300 GDD before silking to ~400 GDD after silking. The 700 GDD

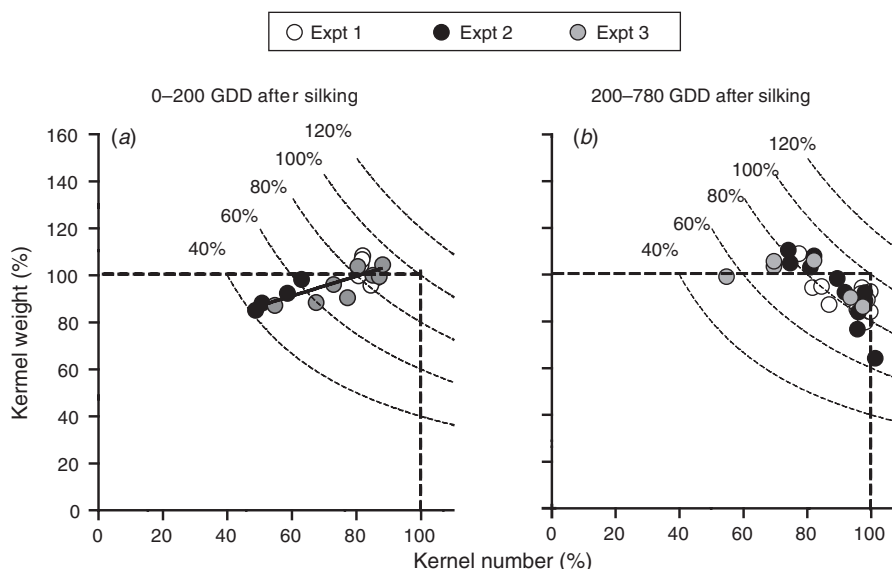


Fig. 3. Relationship between weight per kernel (KW) and kernel number (KN) expressed as a percentage of the control for shading treatments imposed between (a) 0 and 200 growing degree-days (GDD) after silking, and (b) 200 and 780 GDD after silking. Data from all three experiments are presented (Expts 1, 2, and 3). Dotted curves connect points of constant yield (iso-yield) and indicate a percentage of the average of the control. Dashed lines represent the average of KN and KW for the control of the three experiments. Fitted functions: (a) $KW = 0.42 KN + 66$ ($R^2 = 0.61$; $P < 0.001$) and (b) $KW = -0.65 KN + 151$ ($R^2 = 0.53$; $P < 0.001$).

period for KN determination found in this work is wider than expected from previous reports (Claassen and Shaw 1970; Hall *et al.* 1981; Fischer and Palmer 1984; Kiniry and Ritchie 1985; Grant *et al.* 1989; Otegui and Bonhomme 1998). Furthermore, within this period for KN determination, a narrower window of maximum KN responsiveness to resource availability per plant from 200 GDD before silking to 250 GDD after silking was identified. Within this window, Fig. 1*b* appears to indicate a differential susceptibility of KN to resource deprivation according to the precise timing of treatment imposition. Nevertheless, when plant density, shading timing, shading intensity, and year effects were integrated, KN reduction was mainly accounted for by PAR availability per plant. Thus, the accurate temporal analysis allowed the study to establish that the variation in KN during this 450 GDD around silking was mainly accounted for by resource availability and not by timing of stress imposition within this window (Fig. 2*a*). This information should be useful to the design of management practices that affect resource availabilities during this stage of crop development. This information should also be useful to maize crop modelling, particularly to the design of routines for estimating KN.

Kernel weight

Shading before silking did not reduce KW (Fig. 1), indicating no pre-fecundation effect of resource deprivation on potential KW in maize (Borrás and Otegui 2001). Moreover, shading treatments imposed immediately before silking increased KW in Expt 2, probably because of increases in source per kernel during the grain-filling stage.

Shading immediately after flowering reduced not only KN but also KW (Fig. 1, Table 2). Early kernel development in maize is a stage characterised by cell division, cell enlargement, and plastid initiation, which ultimately establish the individual kernel sink capacity (Reddy and Daynard 1983; Ouattar *et al.* 1987; Jones *et al.* 1996; Jones and Setter 2000; Gambín *et al.* 2006; Jia *et al.* 2011). Previous studies conducted under non-restrictive conditions proposed that differences in KW were related to plant growth rate per kernel around the very early stages of grain filling (Gambín *et al.* 2006). This model predicts an increase in potential KW in response to restrictive conditions around flowering that reduce KN proportionally more than plant growth rate (i.e. at low plant growth rates). Our results, however, showed a strong and direct relationship between KW and KN for shading treatments imposed from 0 to 200 GDD after silking (Fig. 3*a*). These results contradict the prediction of the model by Gambín *et al.* (2006) and indicate that when resources per kernel were increased at low levels of resource availability per plant, potential KW was also reduced. Our findings support the hypothesis that potential KW is established during a narrow time-frame immediately after flowering that is included in the time window for KN determination. The simultaneous occurrence of these processes does not allow for a compensation mechanism. Thus, KW increases would not be expected in response to KN reductions originating in restrictive conditions for growth immediately after silking.

Previous local studies found little or no effect of resource deprivation imposed during the effective grain-filling period on yield (Uhart and Andrade 1991; Andrade and Ferreiro 1996; Echarte *et al.* 2006). Nevertheless, Echarte *et al.* (2006) reported that the reduction in KW generated by a severe defoliation at the beginning of the effective grain-filling period increased with the year of hybrid release, and that this reduction was directly related to the ear demand. Accordingly, our results showed for a current hybrid that KW and yield were reduced even by relatively short shading periods during the effective grain-filling period compared with the undisturbed crop (Fig. 1, Table 3), which indicates that restricted plant growth during short periods could not be counterbalanced by assimilate remobilisation. Furthermore, when considering shading imposed beyond the period in which potential KW is established (i.e. beyond 200 GDD), an inverse relationship between yield components was evident (Fig. 3*b*). This inverse relationship presented a small departure from the iso-yield function that represented 80% of the undisturbed crop. The compensation of KN variation with opposite variation in KW indicates that the undisturbed crop for this current hybrid was limited by source capacity during the effective grain-filling period. This was confirmed by the positive response of KW to enhanced assimilate availability per plant by thinning (Table 3). These are novel results when compared with previous studies in which no consistent responses in KW to source increases during the effective grain-filling period were found (Jones and Simmons 1983; Andrade and Ferreiro 1996; Echarte *et al.* 2006), or with a data recompilation study that concluded that maize did not respond to increases in the amount of assimilates per kernel during the grain-filling period (Borrás *et al.* 2004).

Agronomic and breeding prospects

The period around silking is the most critical for yield determination in maize (Figs 1 and 2, Table 3). Kernel number and individual kernel sink capacity (i.e. ear demand) are established during this period (Reddy and Daynard 1983; Jones *et al.* 1996; Gambín *et al.* 2006). Nevertheless, the physiological condition of the crop during the grain-filling stage is becoming more relevant. Based on these results, irrigation scheduling, fertilisation routines, and pest and disease thresholds should be reviewed, especially for cropping systems that explore high productivity levels.

These results would also indicate that future efforts oriented to improve maize potential yield should not only be focussed on sink strength components but also on a simultaneous increase in source capacity during the grain-filling period (Borrás and Gambín 2010; Tollenaar and Lee 2011). Increasing maximum crop growth rate appears to be a difficult task (Tollenaar *et al.* 2000; Ying *et al.* 2000; Lee and Tollenaar 2007; Tollenaar and Lee 2011). Therefore, alternatives to increase source capacity should seek to maintain maximum crop growth rate during grain filling (Lee and Tollenaar 2007; Tollenaar and Lee 2011) or to extend grain-filling duration (Capristo *et al.* 2007). However, at moderate and high latitudes, there is no opportunity to increase total cycle length because of weather restrictions (Capristo *et al.* 2007). At these latitudes, increases in grain-filling duration would be achieved at the expense of the length of the vegetative period.

Additionally, in order to counterbalance the low leaf area per plant, these hybrids that are short to flowering and long to maturity should be planted in denser stands (Sarlangue *et al.* 2007) and at narrow between-row spacing (Andrade *et al.* 2002).

On the other hand, an earlier spring planting would allow an increase in the growing season explored and would allow placement of the grain filling stage under a better radiative and thermal conditions (Cirilo and Andrade 1996). However, this alternative would more likely expose young maize plants to suboptimal temperatures. Therefore, improving the tolerance to low temperature during early stages of development could also be a way to increase source capacity during grain filling (Lee *et al.* 2002).

Conclusions

Grain yield of a recently released maize hybrid was affected by resource availability per plant from before silking to late stages of grain filling. The reduction in resource availability affected KN and KW depending on the stage of crop development. We identified a relatively long period of 700 GDD around silking in which a short resource deprivation reduced KN. Accurate temporal analysis allowed the establishment of a critical period of ~30 days around silking in which KN susceptibility was maximal; within this 30-day window, KN was closely associated with resource availability per plant and not with timing of stress imposition within this window. Additionally, the work showed that for the conditions of these experiments, yield of current hybrids such as the one used in this study appears to be limited by source capacity during the grain-filling period.

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