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Source–sink relations and kernel weight differences in maize temperate hybrids

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Abstract

Maize (*Zea mays* L.) kernel weight (KW) response to changes in assimilate availability per kernel during grain filling suggests that plants establish an early kernel sink potential that place them to grow close to a saturating assimilate availability condition during late grain-filling, meaning source limitations are common only early in kernel development. As maize reproductive efficiency in kernel set is not constant across different plant growth rates (PGR) around flowering, we used PGR per kernel during this period as an indicator of source availability per kernel. We tested whether PGR per kernel during flowering or during the effective grain-filling period were correlated to genotypic and environmental differences in final KW. Plant growth rate during both periods, KW, kernel growth rate during the effective grain-filling period, total duration of grain filling and kernel number per plant were measured in 12 commercial genotypes differing in KW sown at two sites under full irrigation. As expected from the curvilinear response relating kernel number per plant and PGR around flowering, increased PGRs resulted in higher PGR per kernel around this period ($r^2 = 0.86$; $p < 0.001$). Differences in final KW due to genotypes or environments were significantly explained by the PGR per kernel around flowering ($r^2 = 0.40$; $p < 0.001$), and not by the PGR per kernel during the effective grain-filling period. Genotypes differed in kernel growth rate ($p < 0.001$) and grain-filling duration ($p < 0.001$). The former was well explained by PGR per kernel around flowering ($r^2 = 0.66$; $p < 0.001$), but showed no relationship with the PGR per kernel during the effective grain-filling period. Grain-filling duration was partially explained ($r^2 = 0.27$; $p < 0.01$) by the ratio between PGR per kernel during the effective grain-filling period and kernel growth rate, but differences in duration were negligible compared to those observed in the ratio (~41% versus ~130%, respectively). Together, these results support the importance of source availability per kernel during early grain filling on the determination of maize potential sink capacity and final KW. Early resource availability per kernel was accurately estimated as PGR per kernel around the period of kernel number determination, which helped explain genotypic and environmental differences in maize final KW as well as in kernel growth rate.

Keywords: Maize; *Zea mays* L.; Genotypic differences; Grain filling; Source–sink relations; Kernel growth rate

Abbreviations: KW, kernel weight; PGR, plant growth rate

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1. Introduction

In major extensive crops grain yield is mainly determined by the number of harvested kernels per unit land area (Early et al., 1967; Fischer, 1975), being kernel number defined around a period during the crop cycle when grain yield is mostly source limited. Once the number of kernels is established, a yield source–sink co-limitation prevails during grain filling, and the relative importance of this co-limitation varies depending on the species. In a thorough literature review that included a large number of genotypes and environments, Borrás et al. (2004) showed that the pattern of maize kernel weight (KW) response to changes in assimilate availability per kernel during the grain-filling period differed from the pattern obtained for other grain crop species like wheat and soybean. Decreases in the post-flowering source–sink ratio promoted large reductions in final KW, while increasing the ratio had minimum effects in increasing it. This small KW response to increased assimilate availability during the effective grain-filling period suggests that maize plants set an individual kernel sink potential early in grain filling that places further kernel growth close to a saturated assimilate availability condition for biomass accumulation (Borrás et al., 2004). This growth pattern draws attention to the importance of studying the first stages of grain filling in this species.

The typical curvilinear response of kernel number per plant to plant growth rate (PGR) around flowering in maize (Andrade et al., 1999) implies that the intrinsic efficiency of the plant to set kernels declines as PGR increases, especially at PGRs larger than 140–150 mg $^{\circ}$C d^{-1} (Andrade et al., 1999, 2002). This suggests that growing conditions during the period of kernel number determination modify the amount of assimilates available per kernel during their early growing phase, when attributes determinant of kernel sink potential are defined (Capitano et al., 1983; Reddy and Daynard, 1983; Jones et al., 1996). Based on this, we hypothesized that PGR per kernel set around flowering could help estimate source availability per kernel at early grain-filling stages in a simple way. This estimate of source availability per kernel should explain differences in final KW promoted by genotypic or environmental differences if it is true that maize kernels usually grow near saturated assimilate availability conditions during the effective grain-filling period. In turn, kernel growth rate during the effective grain-filling period is the main maize KW determinant (Poneleit and Egli, 1979; Saini and Westgate, 2000; Borrás et al., 2003b), and depends on the sink capacity established early in development (Reddy and Daynard, 1983; Jones et al., 1996). Therefore, if KW differences among genotypes or environments are related to the source availability per kernel prior to the beginning of active kernel growth, they should be explained by the kernel growth rate during the effective grain-filling period.

Knowledge on the physiological mechanisms controlling genotypic differences in the duration of grain filling in maize is well behind those controlling kernel growth rate. It is known that grain-filling duration is reduced when strong source limitations take place during kernel growth (Egharevba et al., 1976; Jones and Simmons, 1983). This shorter grain-filling duration reflects the high dependency on current assimilate production maize kernels have (Kiniry et al., 1992; Borrás et al., 2004), although some genotypic differences exist in the capacity to support KW when assimilates available per kernel are reduced (Borrás and Otegui, 2001). Until present, maize source-sink ratio during grain filling has been classically estimated as biomass produced per kernel during the effective grain-filling period (Uhart and Andrade, 1995; Cirilo and Andrade, 1996; Maddonni et al., 1998; Borrás and Otegui, 2001), without taking into account the actual demand of the growing kernels. In the present study, we analyzed genotypic differences in the ratio between PGR per kernel during the effective grain-filling period (source produced kernel^{-1}) and kernel growth rate (sink demand kernel^{-1}). No information is currently available on how genotypes might differ in this ratio or if it might be behind genotypic differences in the duration of grain filling.

The present work was carried out for testing the above stated hypothesis using a wide range of current commercial genotypes differing in final KW. Field experiments were conducted at two experimental sites under full irrigation.

2. Materials and methods

The experiments were conducted at two sites: the experimental field of the Department of Plant

Production at the University of Buenos Aires (35°35′S, 59°29′W), and the Experimental Field of Nidera Argentina S.A. in Venado Tuerto (32°40′S, 61°58′W), during the 2003/2004 growing season. Soils were of the silty clay loam type, a Vertic Argiudoll at Buenos Aires (BA) and a Typic Hapludoll at Venado Tuerto (VT). Twelve single-cross maize hybrids (Ax610 MG, Xa0675 MG, Ax800 MG, Ax820 MG, Ax832 CL-MG, Ax842 MG, Ax877 MG, Ax878 MG, Ax882 MG, Ax888 CL-MG, Ax889 MG, Ax890 MG) were used, which differed in final KW and endosperm type. Most were commercial hybrids (Nidera Argentina, 2003) developed from a total of 13 elite inbred lines of the Nidera Argentina S.A. breeding program for the central maize region of Argentina. The pre-commercial hybrids were Ax878 MG and Xa0675MG.

At both sites, treatments were arranged in a randomized complete block design with three replicates. Each replicate involved five rows 0.5 m apart and 5 m long at BA, and five rows 0.7 m apart and 15 m long at VT. Sowing took place on 1 October at BA and on 30 October at VT. Plots were over sown and thinned at the three-leaf stage (ligulated leaves) to a stand density of 90,000 plants ha^{-1}. Nitrogen was applied at a rate of 100 kg ha^{-1} per application. Two applications were made at BA (at the four-leaf stage and on ca. 15 days before flowering) and one at VT (on ca. 15 days before flowering). Experiments were conducted under no visible water stress, and pests and weeds were adequately controlled throughout the growing cycle. Water stress was prevented by means of furrow (BA) or sprinkler (VT) irrigation, maintaining the soil near field capacity throughout the growing season.

In each experiment, 30 plants per replicate were tagged at random 15 days before male flowering (i.e. anthesis). Silking date (i.e. first silk visible) of the apical ear was registered for all tagged plants. Beginning on 7 days after silking, the apical ear shoot of one plant per replicate was harvested every 4–6 days. Samples consisted of 10–15 kernels from the same ear position (between spikelets 10 and 15 from the bottom of the apical ear). Kernel weight comparisons were always based on this same position in order to avoid possible confounding effects associated with floret positions within the rachis or genotypic differences in the proportion of apical and basal kernels when whole mean ear kernel weights are used. Dry weights were determined after drying the kernels in an air-forced oven at 70 °C for at least 96 h.

Final KW, kernel growth rate during the effective grain-filling period and total duration of grain filling were determined for each genotype at each site by fitting a bilinear model (Eqs. (1) and (2)):

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

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

where TT is thermal time after silking (in °Cd), a the Y-intercept (in °Cd), b the kernel growth rate during the effective grain-filling period (in mg $°Cd^{-1}$), and c the total duration of grain filling (in °Cd). The bilinear model was fitted to the kernel dry weight data using the iterative optimization technique of Table Curve V 3.0 (Jandel Scientific, 1991). Daily TT values were obtained with a base temperature of 0 °C (Muchow, 1990). Mean daily air temperature was calculated as the average of hourly air temperatures registered at a weather station located at approximately 50 m from the experimental plots at both sites.

Non-destructive allometric models (Vega et al., 2000, 2001; Borrás and Otegui, 2001) were used for the estimation of plant biomass at two stages of the growing cycle: 15 days pre- and 15 days post-flowering. The fifteen days pre-flowering stage was estimated as the moment when five leaves were still to be expanded, and the 15 days post-flowering as 15 days after 50% of the plants reached silking. The allometric approach was used in order to always ensure the closest representation of plant biomass corresponding to tagged plants that remained in the field until final harvest. Models were developed from three or four additional tagged plants per replicate harvested for each hybrid at each site at pre- and post-flowering. 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 ranged between 0.82 and 0.98 ($p < 0.001$) at BA, and between 0.86 and 0.98 ($p < 0.001$) at VT. The post-flowering model involved stem volume and maximum apical ear diameter, and it was fitted for each genotype and site using a multiple regression analysis. For a detailed

description of this model see Borrás and Otegui (2001). The range of r^2 values for this model was between 0.74 and 0.96 ($p < 0.001$) at BA, and between 0.81 and 0.99 ($p < 0.001$) at VT. The pre- and post-flowering allometric models were used to estimate the biomass of four plants per replicate that remained in the field until physiological maturity. At this stage (defined as 75% milk line; Hunter et al., 1991) these plants were harvested and individual kernel number per plant determined by manual counting. Shoot biomass was always obtained after drying plants in an air-forced oven at 65 °C for at least 1 week.

Plant growth rate around flowering (in mg °Cd^{-1}) was calculated as the ratio between plant biomass increase (mg) from silking −15 d to silking +15 d and

Table 1
Plant growth rate (PGR) around flowering, kernel number per plant, PGR per kernel around flowering, PGR per kernel during the effective grain-filling period, final kernel weight (KW) from spikelet positions 10–15 from the bottom of the apical ear, kernel growth rate during the effective grain-filling period, and total grain-filling duration of 12 commercial genotypes differing in final KW tested at two sites, Buenos Aires (BA) and Venado Tuerto (VT)

Genotype	Site	PGR around flowering (mg °Cd^{-1})	Kernel number per plant	PGR per kernel around flowering (mg °Cd^{-1} kernel^{-1})	PGR per kernel during the effective grain-filling period (mg °Cd^{-1} kernel^{-1})	KW (mg)	Kernel growth rate (mg °Cd^{-1} kernel^{-1})	Total grain-filling duration (°Cd)
Ax610 MG	BA	171	484	0.36	0.22	299	0.30	1189
	VT	273	501	0.55	0.14	281	0.34	1045
Xa0675 MG	BA	224	511	0.44	0.23	346	0.34	1266
	VT	307	505	0.58	0.21	380	0.41	1235
Ax800 MG	BA	216	560	0.39	0.17	304	0.30	1323
	VT	251	469	0.54	0.17	330	0.36	1249
Ax820 MG	BA	201	495	0.41	0.20	318	0.33	1234
	VT	263	531	0.50	0.21	330	0.33	1247
Ax832 CL-MG	BA	174	540	0.33	0.17	268	0.24	1366
	VT	282	596	0.47	0.15	294	0.30	1382
Ax842 MG[a]	BA	188	495	0.38	0.25	365	0.30	1470
	VT	269	596	0.46	–	–	0.33	–
Ax877 MG	BA	211	598	0.36	0.15	280	0.26	1337
	VT	275	577	0.48	0.21	339	0.33	1384
Ax878 MG	BA	182	546	0.33	0.19	311	0.29	1325
	VT	254	613	0.41	0.15	288	0.33	1162
Ax882 MG	BA	176	586	0.33	0.23	293	0.28	1295
	VT	261	563	0.45	0.21	309	0.35	1158
Ax888 CL-MG	BA	194	509	0.38	0.19	287	0.30	1138
	VT	321	585	0.55	0.14	308	0.31	1251
Ax889 MG	BA	247	507	0.48	0.18	297	0.36	1117
	VT	339	506	0.67	0.21	352	0.40	1160
Ax890 MG	BA	316	493	0.64	0.12	344	0.37	1314
	VT	342	543	0.62	0.15	351	0.45	1129
Site mean	BA	208	527	0.40	0.19	309	0.31	1281
	VT	286	549	0.52	0.18	324	0.35	1218
Genotype (G)		(39)[b,***]	(49)[**]	(0.06)[***]	(0.03)[***]	(27)[***]	(0.04)[***]	(106)[***]
Site (S)		(28)[**]	NS	(0.03)[***]	NS	NS	(0.02)[**]	NS
G × S		NS	(70)[*]	NS	(0.04)[***]	NS	NS	NS

NS: not significant.

[a] The hybrid Ax842 MG was excluded from the statistical analysis for PGR per kernel during the effective grain-filling period, KW and total duration of grain-filling because of wind logging before physiological maturity at VT.

[b] LSD value for $p \leq 0.05$.

[*] $p = 0.05$.

[**] $p = 0.01$.

[***] $p = 0.001$.

the thermal time interval between these sampling dates. Daily thermal time values for this stage were calculated using a base temperature of 8 °C (Ritchie and NeSmith, 1991). Plant growth rate per kernel around flowering (in mg °Cd^{-1} kernel^{-1}) 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 (in mg °Cd^{-1}) was obtained as the quotient between shoot biomass increase (mg) from silking +15 d up to physiological maturity and the thermal time interval between these stages. Daily thermal time values for this period were calculated with a base temperature of 0 °C (Muchow, 1990). Plant growth rate per kernel during the effective grain-filling period (in mg °Cd^{-1} kernel^{-1}) was calculated as the ratio between PGR during this period and the number of kernels per plant.

Analysis of variance was used to evaluate the effects of genotypes, sites and their interactions on the response variables as a randomized complete block design with three replicates combined over sites. Linear regression analysis was applied to the relationships among variables. The hybrid Ax842 MG was excluded from analyses concerning KW and duration of grain filling because of wind logging before physiological maturity at VT.

3. Results

Genotypes differed in PGR around flowering ($p < 0.001$; Table 1), and these differences were very consistent in both environments in spite of the significant site effects ($p < 0.01$). Mean values of PGR around flowering were lower at BA than at VT (Table 1), and ranged between 171 and 316 mg °Cd^{-1} for the former, and between 251 and 342 mg °Cd^{-1} for the latter. Genotypes also differed in the number of kernels set per plant ($p < 0.001$), but a genotype *x* site interaction was detected for this trait ($p < 0.05$; Table 1). Genotypes showed no prolificacy, so kernel numbers were always from the uppermost ear. Averaged across genotypes and environments, the range explored for this trait varied between 469 and 613 kernels plant^{-1} (Table 1). In spite of this range, kernel number per plant showed no response to the large variation in PGR around flowering (Fig. 1A) when all the genotype *x* site combinations were plotted together.

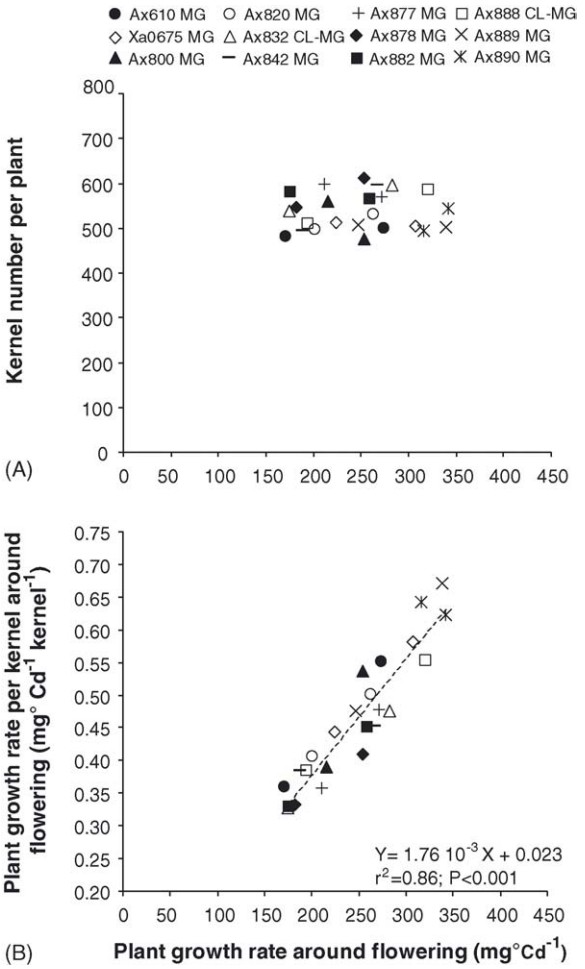

Fig. 1. Relation between kernel number per plant and plant growth rate around flowering (A), and between plant growth rate per kernel and plant growth rate around flowering (B). Data correspond to 12 commercial hybrids differing in final kernel weight evaluated at two sites. Each symbol represents the mean of three replicates, where four plants per replicate were sampled. Individual plant growth rate was estimated by means of allometric models.

Variations in PGR around flowering and in the number of kernels set per plant produced a wide range of PGRs per kernel around this period, leading to genotypic ($p < 0.001$) and site ($p < 0.001$; Table 1) significant differences. Values of PGR per kernel around flowering varied from 0.33 to 0.64 mg °Cd^{-1} kernel^{-1} in BA, and from 0.41 to 0.67 mg °Cd^{-1} kernel^{-1} in VT. When data from all tested genotypes

and sites were pooled together, increases in PGR around flowering always led to increases in PGR per kernel ($r^2 = 0.86$; $p < 0.001$; Fig. 1B), as expected from Fig. 1A and as a result of the curvilinear response between kernel number per plant and PGR bracketing flowering when PGR values are higher than 140–150 mg °Cd^{-1}. During the effective grain-filling period, PGR per kernel also showed significant genotypic differences ($p < 0.001$), although a significant genotype *x* site interaction was found ($p < 0.001$; Table 1). The range explored of PGR per kernel during the effective grain-filling period was between 0.12 and 0.25 mg °Cd^{-1} kernel^{-1} across all genotype × site combinations. Thus, genotypes and sites helped explore a wide range of PGR per kernel during both early and late grain filling.

Averaged across sites, final KW from spikelet positions 10 and 15 from the bottom of the apical ear showed a wide range among genotypes ($p < 0.001$; Table 1), which varied from 281 to 365 mg kernel^{-1}. Genotypes differed in both, kernel growth rate during the effective grain-filling period ($p < 0.001$) and total duration of grain filling ($p < 0.001$; Table 1). Genotypic means for kernel growth rate ranged between 0.27 and 0.41 mg °Cd^{-1} kernel^{-1} (between 5.9 and 9.9 mg d^{-1} kernel^{-1}). The environment, however, promoted significant differences ($p < 0.01$) in kernel growth rate. Averaged across genotypes, this rate was lower at BA (0.30 mg °Cd^{-1} kernel^{-1}) than at VT (0.36 mg °Cd^{-1} kernel^{-1}). Genotypic differences in total duration of grain filling ranged between 1045 and 1470 °Cd^{-1}, with no significant differences between sites (Table 1). When all genotype *x* site combinations were pooled, KW differences were only related to kernel growth rate during the effective grain filling period ($r^2 = 0.44$; $p < 0.001$; $n = 23$). No relationship was observed between final KW and total duration of grain filling, in spite of the genotypic differences registered for the latter. Although final KW was strongly related to kernel growth rate during the effective grain-filling period and VT showed higher rates than BA, there was only a trend for higher final KWs at VT ($p < 0.07$; Table 1). This might be related to the negative correlation observed between kernel growth rate and grain-filling duration for the whole data set ($r^2 = 0.39$; $p < 0.003$; $n = 23$).

Variations due to genotypes and environments in final KW detected at physiological maturity were significantly correlated with PGR per kernel set around flowering ($r^2 = 0.40$; $p < 0.001$; Fig. 2A). There was no relation between final KW and PGR per kernel during the effective grain-filling period (Fig. 2B). These results indicate that differences in

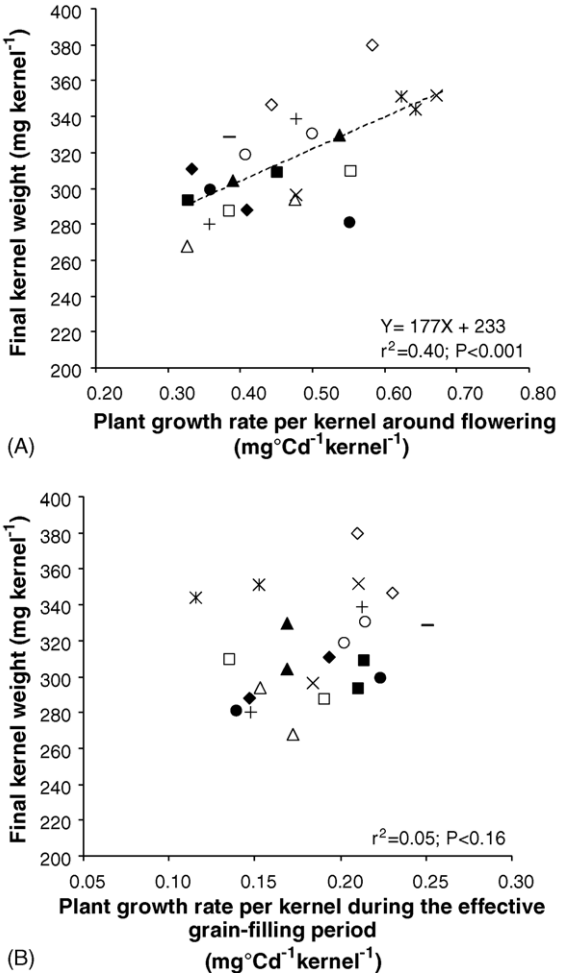

Fig. 2. Relation between final kernel weight and plant growth rate per kernel around flowering (A), and between final kernel weight and plant growth rate per kernel during the effective grain-filling period (B), for all genotypes at both sites. Symbols as in Fig. 1. Data for hybrid Ax842 MG at VT was not included because of plant logging before the end of grain filling. Kernel weight was always measured from the same ear position (spikelets 10–15 from the bottom of the apical ear), and final kernel weight was calculated using a bilinear with plateau model fitted to each genotype × site combination. Plant growth rate was calculated with a base temperature of 8 °C around flowering and with a base temperature of 0 °C during the effective grain-filling period.

KW were associated with the amount of resources available per kernel early in grain filling but not during the effective grain-filling period.

Differences in kernel growth rate during the linear phase of kernel growth were strongly related to PGR per kernel around flowering ($r^2 = 0.66$; $p < 0.001$; Fig. 3A). There was no relationship between kernel growth rate during the effective grain-filling period and PGR per kernel during this stage (Fig. 3B). This indicated plant growth per kernel during the *lag* phase, and not from the *lag* phase onwards, was the promoter of the kernel growth rate variations observed among genotypes and environments. Nevertheless, although differences in KW were mainly related to changes in kernel growth rate ($p < 0.001$), genotypic differences in grain-filling duration were evident (Table 1). These genotypic differences in grain-filling duration determined that conditions early in grain filling, represented as PGR per kernel around flowering, helped explain 66% of the variation in kernel growth rate (Fig. 3A) but only 40% of the total variation in KW (Fig. 2A).

Genotypic differences in total duration of grain filling were related to variations in the ratio between PGR per kernel during the effective grain-filling period and kernel growth rate during the same stage ($r^2 = 0.27$; $p < 0.01$; Fig. 4). As both rates varied across hybrids and sites, we hypothesized that the relation between them would serve as a good estimate of the source–sink ratio during the last part of grain filling. A trend was detected for longer grain-filling durations under higher source–sink ratios during the effective grain-filling period, which helped explain the observed negative correlation between kernel growth rate and grain-filling duration. This trend, however, had minor effects on KW at physiological maturity (Table 1), as the genotypic variation observed for the ratio was very large (between 0.35 and 0.80), and was

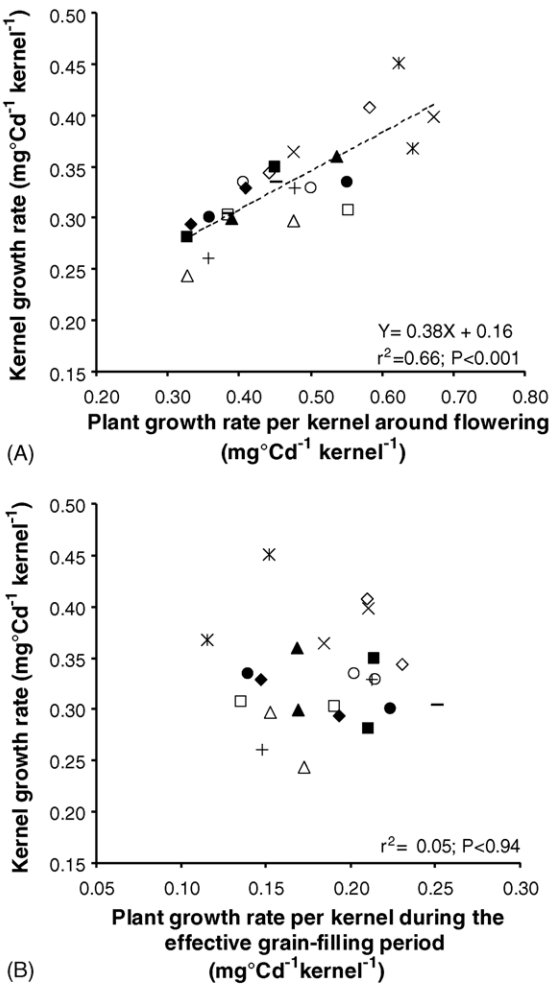

Fig. 3. Relation between kernel growth rate and plant growth rate per kernel around flowering (A), and between kernel growth rate and plant growth rate per kernel during the effective grain-filling period (B), for all genotypes at both sites. Symbols as in Fig. 1. Kernel growth rate was calculated using a bilinear with plateau model.

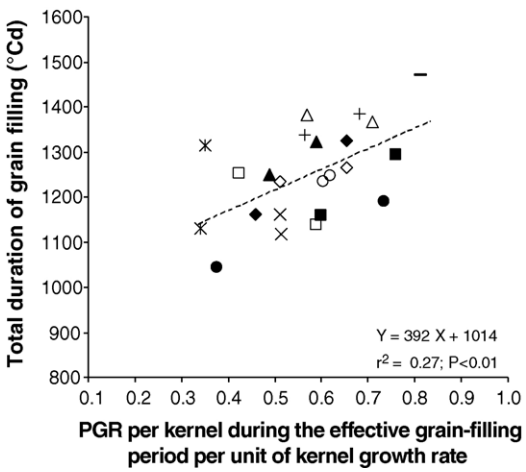

Fig. 4. Relation between total duration of grain filling and the ratio between plant growth rate per kernel during the effective grain-filling period and kernel growth rate along the same stage for all genotypes and sites. Symbols as in Fig. 1.

not matched by a comparable variation in grain-filling duration (between 1045 and 1470 °Cd).

4. Discussion

The source–sink ratio around the period of kernel number determination, measured as PGR per kernel set, explained the variations observed in maize final KW (Fig. 2A). Conversely, KW was not conditioned by the PGR per kernel during the effective grain-filling period (Fig. 2B). These results support our current working hypothesis as well as previous evidence on this topic (Borrás et al., 2004), indicating that maize plants set an individual kernel sink potential during early kernel development that places further kernel growth close to a condition of saturation in assimilate availability for biomass accumulation.

The lack of a positive correlation between kernel number per plant and plant growth rate around flowering (shown in Fig. 1A) was not expected, but was not a surprise either. At present, relations between kernel number and PGR are usually shown for single genotypes (Andrade et al., 1999, 2002; Echarte et al., 2004), and from these studies we have learned that each genotype has its own kernel number response pattern to changes in PGR. Our attempt to place 12 genotypes together has drawn attention in the existing wide variability in PGR around flowering leading to similar kernel numbers, giving light to important genotypic differences in biomass partitioning to the ear or in reproductive efficiency in kernel set. Moreover, recent results suggest that biomass partitioning to the ear is not only related to total plant growth (Xu et al., 2004). These are critical issues for further kernel number improvement in temperate germplasm.

Genotypic differences in KW were related to the extremely dynamic source–sink relations taking place during the first stages of kernel development. These findings highlight the importance of early grain filling stages in the determination of potential KW, and support previous evidence on differences in final KW in relation to the number of endosperm cells or amyloplasts produced during the *lag* phase (Tollenaar, 1977; Capitano et al., 1983; Reddy and Daynard, 1983; Jones et al., 1996). Previous research in maize individual kernel sink potential (Reddy and Daynard, 1983; Ober et al., 1991; Jones et al., 1996) have shown that kernel growth conditions (i.e. the resource availability per kernel) early in grain development influenced their later growth. In the present study, we used a simple source–sink ratio estimation based on the intrinsic maize plant efficiency to set kernels at different PGR levels around flowering, and we showed that, even considering possible sources of error from methodology, it was strongly determinant of final KW for a large number of contrasting commercial genotypes grown at different environmental conditions. An enhanced source–sink ratio around flowering yielded an increased final KW through changes in the kernel growth rate during the effective grain-filling period (Fig. 3A). Differences in kernel growth rate are usually related to differences in early kernel sink capacity (Capitano et al., 1983; Reddy and Daynard, 1983; Jones et al., 1996; Borrás et al., 2003b), supporting our hypothesis. Although in the present study we did not discriminate between pre- and post-flowering effects, previous evidence showed there are no pre-fecundation effects over potential kernel size in maize (Borrás and Otegui, 2001), suggesting the early post-flowering period to be the only critical one.

The present study has mainly addressed ecophysiological processes behind genotypic differences in KW. Our findings on the importance of PGR per kernel around flowering could help explain variations in this grain yield component promoted by other factors not evaluated in our study when placed in the theoretical frame we propose for maize potential KW determination (Fig. 5). Examples of this are (i) stand density treatments, where plants growing at reduced crowding (i.e. right side of the *x* axis in Fig. 5A and B) set an increased number of kernels that are filled at larger kernel growth rates and reached larger final KWs than their counterparts growing at high plant populations (Borrás and Otegui, 2001; Borrás et al., 2003a,b), (ii) drought treatments imposed only around the flowering period, where drought reduces kernel number as well as final KW (Hall et al., 1981; Chapman and Edmeades, 1999), or (iii) KW and kernel growth rate changes promoted by pollination treatments performed during the kernel set period and aimed to alter the number of kernels set by the plant (Borrás and Otegui, 2001; Schussler et al., 2002; Borrás et al., 2003a,b). Stand density or drought conditions around flowering are known to affect the

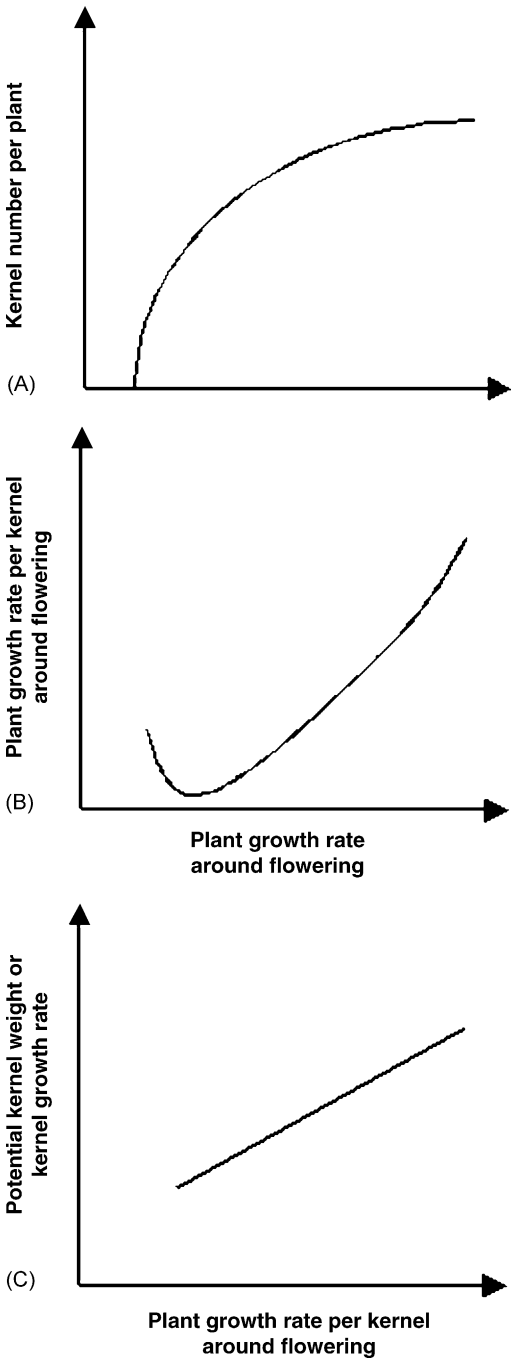

Fig. 5. Schematic diagram of the theoretical frame proposed for the determination of genotypic and environmental differences in maize kernel sink potential. Environmental conditions affect kernel set through changes in plant growth rate around flowering (A). This relationship affects the plant growth rate per kernel (i.e. resource availability per kernel) early in their development (B), making kernels establish a differential kernel sink potential (C). Genotypic differences in the relation between kernel number per plant and plant growth rate around flowering (A) would impact the resource availability per kernel (B) and kernel sink potential (C). For simplification (A) only shows the number of kernels set per plant from the apical ear, but appearance of secondary ears at large plant growth rates would impact resource availability per kernel (B) and kernel sink potential (C) also.

PGR around that period, affecting the PGR per kernel and the final KW. Pollination treatments affect the number of kernels for the same plant growing condition (i.e. PGR around flowering), so the same amount of assimilates produced around flowering is distributed over a different kernel number (i.e. variation along the *y* axis of Fig. 5A with no variation along the *x* axis). These pollination treatments have shown to decrease KW and kernel growth rate whenever kernel number per plant was increased, and to increase them whenever the number of kernels was reduced, following the concept of PGR per kernel around flowering as the driving force of KW differences. Last, the increase in PGR per kernel at low PGRs close to the PGR threshold value for kernel number determination is supported by the large KW variability observed in plants with reduced shoot biomass at physiological maturity bearing very low kernel numbers (Echarte and Andrade, 2003).

Genotypic differences in total duration of grain filling seemed to be associated with a different capacity of the genotypes to maintain a high post-flowering plant biomass production per kernel in relation to the rate of biomass accumulation within each kernel. The duration of grain filling tended to be longer for those genotypes having higher ratios between PGR per kernel and kernel growth rate during the effective grain-filling period (Fig. 4). Although the same interpretation can be used to understand differences in total duration of grain filling whenever assimilate availability per kernel is reduced (Egharevba et al., 1976; Jones and Simmons, 1983; Borrás et al., 2004), it is known that increased source availability per kernel during the effective grain filling period has no effect over the total duration of grain-filling (Schoper et al., 1982; Andrade and Ferreiro, 1996; Borrás et al., 2003b). Further studies are needed to define the mechanisms controlling the duration of grain filling in maize genotypes with special attention to the observed large genotypic variability in the ratio

between the rate of total biomass production per kernel and the rate of kernel growth during the effective grain-filling period.

5. Conclusions

Differences in maize KW due to genotypes or environments were related to the source–sink ratio established around the very early stages of grain filling, and these differences were associated with changes in kernel growth rate during the effective grain-filling period. Plant growth rate per kernel around flowering served to estimate this source–sink ratio. The present findings show the importance of the period around flowering not only in the definition of kernel number per plant, but also in potential KW. This reveals the period around flowering to be more critical in the establishment of the potential grain yield in this species than it has been assumed until present. We believe the present work provides new insights in KW determination that can be used for a more mechanistic, yet simple, definition of KW determinants (i.e. rate and duration of grain filling) than currently used in broadly adopted simulation models like CERES maize (Jones and Kiniry, 1986).

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