



Maize grain yield components and source–sink relationship as affected by the delay in sowing date



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ABSTRACT

Delaying maize (*Zea mays* L.) sowing date can diminish grain yields through reductions in the number, size and activity of growing grains (sink strength) and/or reductions in the assimilate supply (source capacity) to grains during the grain filling period. Whether the source capacity or the sink strength is the limiting factor for grain yield in late sown maize still remains unclear. Understanding source–sink relationships is relevant to optimize crop management practices, to identify critical processes for crop modelling and to develop breeding strategies. The objective of this work was to assess the effect of delays in maize sowing date on grain yield components and on the source–sink relationship during the grain filling period. Three well irrigated and fertilized maize field experiments were conducted at Balcarce, Argentina (37° 45' S, 58° 18' W; 130 m a.s.l.) during 2009–10; 2010–11 and 2011–12 cropping seasons. Sowing dates ranged from October to January covering a broad range of the seasonal photo–thermal variation. Grain yield was affected by sowing date and varied from 1680 g m⁻² (early sowings) to 203 g m⁻² (late sowings). Grain number per unit area was reduced proportionally less than weight per grain as sowing date was delayed. Variations in grain yield were related to the harvest index, and were closely associated with dry matter accumulation during the post-silking period. The variation of source capacity was higher than that of sink strength during the grain filling period and the source/sink ratio decreased from early to late sowing dates. Results indicate that crop growth during the grain filling period was limited by the sink strength in early sowing dates and by the photosynthetic source capacity in the late ones.

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1. Introduction

Sowing date is one of the main management practices used to adjust the timing of occurrence of crop phenological phases and therefore, to determine the environmental conditions under which crops develop and grow. Changes in maize sowing date alter crop growth rate and the length of crop phenological phases which, in turn, modify potential grain yield and its components (Cirilo and Andrade, 1994a). These alterations are particularly significant in cool-temperate short season environments, where solar radiation

and temperature change considerably around the beginning and the end of the maize cropping season (Shaw, 1988; Wilson et al., 1995).

Variations in grain yield can be analyzed in terms of the crop carbon economy during the grain filling period. This approach, commonly described as source–sink relationship, aims to identify when grain yield is limited by the supply (source capacity) or by the demand (sink strength) of assimilates during the grain filling period (Tollenaar, 1977). In maize, source capacity is mainly determined by assimilate production by crop photosynthesis during the grain filling period. Sink strength is defined by the ability of the growing grains to accommodate these assimilates. Maize grain yield has been generally reported as to be sink limited (Tollenaar and Lee, 2011; Westgate et al., 2004). As a consequence, most recommended management practices (Andrade et al., 2005) and major breeding efforts in maize (Echarte et al., 2000; Tollenaar et al., 1992) have been focused in maximizing the number of grains per unit area.

Abbreviations: ECG, end of crop growth; RUE, radiation use efficiency; TT, thermal time; PAR, photosynthetically active radiation; EGFP, effective grain filling period; CGR, crop growth rate; GGR, grains growth rate; HI, harvest index; fi, fraction of intercepted PAR; RMSE, root mean square error.

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In temperate and cool-temperate environments, when maize sowing is delayed, crop flowering occurs far after the summer solstice and grain filling period takes place close to the end of the cropping season. Thus, as sowing date is delayed in these environments, both the critical period for grain set and the grain filling period are subjected to a progressive deterioration of photo-thermal conditions for crop growth. In accordance, delays in maize sowing date can diminish grain yields through reductions in: i) the number, size and activity of growing grains and/or ii) the assimilate production by photosynthesis during the grain filling period (Cirilo and Andrade, 1996, 1994b; Tsimba et al., 2013a).

Information about grain yield components and source-sink relationships during the grain filling period helps in the selection and optimization of key crop management practices such as hybrid selection, plant density, irrigation strategies, crop protection, etc. (Andrade et al., 2005). This information is also relevant to identify critical processes for crop modelling and to develop breeding strategies (Hall and Sadras, 2009). Previous investigations on maize sowing date have described grain yield components and, to some extent, indicative variables of the source-sink relationship during the grain filling period. However, whether the source capacity or the sink strength is the limiting factor to grain yields in late sown maize still remains unclear. The objective of this work was to assess the effect of sowing date delays on maize grain yield components and on the source-sink relationship during the grain filling period.

2. Materials and methods

2.1. Site description and crop management

Three experiments were conducted at INTA-Balcarce experimental station, Argentina (37° 45' S, 58° 18' W; 130 m a.s.l.) during 2009–10 (Exp. 1), 2010–2011 (Exp. 2) and 2011–2012 (Exp. 3) cropping seasons. Data of two complementary experiments conducted during 2012–13 (C. Exp. I) and 2011–12 (C. Exp. II) were also included in an analysis that merged all observed grain yields. Experiments were established on a fine-loamy typic argiudol with an effective depth of 1.5 m. Topsoil organic matter was 5.6% and extractable phosphorous content was 32 ppm. The field was managed under conventional tillage in Exp. 1 and under no-till in Exp. 2, Exp. 3, C. Exp. I and C. Exp. II. Wheat (*Triticum aestivum* L.) was the previous crop in all instances.

Plots were over-sown with hand planters and were thinned to a uniform plant population immediately after V₂ crop phenological stage (Ritchie et al., 1989). Final plant population was 8.7 plants m⁻² in Exp.1 and 10 plants m⁻² in Exp. 2, Exp. 3, C. Exp. I and C. Exp. II. Rows were 0.52 m apart. Soil water content was kept above 65% of the maximum soil available water by complementing precipitations with sprinkler irrigation. In order to provide an adequate mineral nutrition, plots were fertilized before sowing with 30 kg of P ha⁻¹ (diammonium phosphate). A mix of 50 kg of S ha⁻¹ (calcium sulfate) and 400 kg N ha⁻¹ (urea) was also applied in three equal splits at i) emergence, ii) V₅ and iii) R₁ crop phenological stages. Potassium requirement was assumed to be covered by the natural abundance of K⁺ in the illite-rich soils where experiments were conducted. Weeds, insects, and diseases were effectively controlled.

2.2. Plant material and experimental design

Three commercial hybrids were used: P39B77 Herculex® LibertyR® (relative maturity rating: 92; Pioneer, Arg.), I550 MGRR2 (relative maturity rating: 102; Illinois, Arg.) and DK692 MGRR2 (relative maturity rating: 119; DeKalb, Arg.). In Exp. 1, the hybrid P39B77 was tested in a randomized complete-block design with

two replications. Treatments consisted of seven sowing dates ranging from November to January. Plots were four rows wide by 10 m long. In Exp. 2 and C. Exp. I, the hybrid DK692 was tested in a randomized complete-block design with four replications. Treatments consisted of four contrasting sowing dates ranging from October to January. In Exp. 3, hybrids P39B77, I550 and DK692 were tested in a split-plot randomized design with four replications. Treatments involved the factorial combination of four contrasting sowing dates (main plot) and the three abovementioned hybrids (subplot). In C. Exp. II, a total of 16 commercial hybrids sown on a single sowing date (Oct-3) were tested in a randomized complete-block design with three replications. Plots in Exp. 2, Exp. 3, C. Exp. I and C. Exp. II were nine rows wide by 12 m long. Sowing dates and hybrids of three main experiments are detailed in Table 1.

2.3. Measurements and estimations

2.3.1. Crop phenology

Crop phenological stages were determined according to Ritchie et al. (1989). Number of expanded leaves was weekly recorded from emergence to V_T in five plants per plot. Leaves number 5 and 10 were paint-marked to keep a leaf number reference. Duration of phenological stages was expressed in days and in thermal time (TT) units. Daily TT degrees were calculated as follows (Eq. (1)) and accumulated between phenological stages:

$$TT (^{\circ}\text{Cd}^{-1}) = \frac{T_{\text{max}} + T_{\text{min}}}{2} - T_b \quad (1)$$

where T_{max} and T_{min} are daily maximum and minimum temperatures, respectively. The base temperatures (T_b) for TT estimations were previously estimated following the methodology described by Tsimba et al. (2013b). Briefly, a T_b -iterative procedure was performed to find the lowest TT CV% for each of the main phenological phases of each hybrid across sowing dates and growing seasons. The most accurate T_b did not differ from 10 °C (for emergence to silking period) and 0 °C (for silking to physiological maturity). These T_b were in agreement with those proposed by Tollenaar et al. (1979) for the pre-silking period and by Birch et al. (1998) and by Muchow (1990) for the post-silking period.

Grain samples were taken every 7–10 days starting at 10 days after 50% silking and ending at least three weeks after black layer formation. At each sampling date 15 grains were taken from the central portion of two ears per plot. A total of 8 different plants (two plants by 4 blocks) were randomly selected at each sampling date. Grains were dried at 90 °C for 7–10 days in an air forced oven and weighed. Mean growth rate per grain and duration of effective grain filling period (EGFP) were estimated following the lineal-plateau fitting method (in which the weight per grain is expressed as a function of the days after silking) described by Egli (1998). Physiological maturity¹ was estimated as the day when the maximum weight per grain was achieved.

2.3.2. Dry matter accumulation, PAR interception and grain yield

Aboveground dry matter was periodically measured in Exp. 2 and Exp. 3 by taking samples of 8–10 plants (sample area of about 1 m²) from the five central rows. A total of 5–6 samples were taken every 15–25 days during each crop cycle. Three to four plants were left as border between successive samples. Aboveground dry matter in Exp. 1 was determined at harvest from 10 plants (sample area

¹ The “physiological maturity” term in the current work is used to refer to the moment when grains stopped growing, even for those cases of premature cessation of grain growth. We also used the term “end of crop growth” (ECG) to refer to the moment at which crop aboveground dry matter accumulation ceased, which may not be coincident with physiological maturity (Uhart and Andrade, 1991).

Table 1

Duration of crop phenological stages, mean temperature and final number of leaves of contrasting maturity maize hybrids at different sowing dates in Balcarce (37° 45' S, 58° 18' W). Durations are expressed in days (d) and thermal time units (TT). Base temperatures for thermal time estimations were 10 °C for emergence-silking period and 0 °C for silking-physiological maturity period.

Exp.	Sowing date	Hybrid	Emergence to silking period			Silking to Phys. Maturity period			Final leaf number
			duration		mean temp.	duration		mean temp.	
			d	TT	°C	d	TT	°C	
1 (2009–10)	Nov-16	P39B77	56	553	19.9	50	1048	21.4	17.0
	Dec-11	P39B77	48	568	22.4	59	1123	19.1	17.0
	Dec-22	P39B77	47	561	22.6	54	974	18.0	17.5
	Dec-29	P39B77	46	544	22.4	58	1020	17.6	17.0
	Jan-05	P39B77	48	533	21.5	55	936	17.0	17.0
	Jan-12	P39B77	49	540	21.4	45	756	16.8	17.0
	Jan-20	P39B77	51	533	20.7	36	590	16.4	16.5
		Sowing date	***	***	–	***	***	–	***
		(1.7)	(19.6)	–	(2.2)	(34.9)	–	(0.3)	
1 (2010–11)	Oct-4	DK692	92	770	18.1	58	1228	21.4	21.4
	Nov-2	DK692	72	731	20.1	55	1139	21.0	21.9
	Dec-1	DK692	66	728	21.4	60	1167	19.6	21.8
	Jan-3	DK692	61	683	21.4	67	1070	16.0	20.2
		Sowing date	***	***	–	***	***	–	**
		(1.9)	(23)	–	(1.9)	(32)	–	(0.6)	
3 (2011–12)	Oct-4	P39B77	75	618	17.8	50	1109	23.3	17.2
		I550	82	702	18.3	52	1133	22.7	19.2
		DK692	86	752	18.6	57	1233	22.3	21.0
	Nov-14	P39B77	54	555	20.6	49	1059	22.4	17.6
		I550	60	634	21.0	53	1140	22.1	19.3
		DK692	67	713	21.0	59	1220	21.2	21.0
	Dec-15	P39B77	50	596	22.7	50	975	19.8	17.9
		I550	57	678	22.8	60	1120	18.7	20.0
		DK692	60	719	22.9	59	1085	18.4	21.8
	Jan-4	P39B77	51	600	22.5	59	1012	17.2	17.4
		I550	58	682	22.4	54	878	16.3	18.6
		DK692	65	762	22.3	69	1006	14.6	20.8
		Sowing date	***	***	–	***	***	–	***
		Hybrid	***	***	–	***	***	–	***
		Sowing date × Hybrid	***	***	–	***	***	–	NS
			(2)	(24.5)	–	(2.4)	(40.6)	–	(0.31)

ANOVA *p*-values: **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

NS: not significant.

LSD values for mean comparison are presented in brackets.

of about 1.15 m²) of two central rows per plot. After each sampling, plants were immediately oven dried (60–70 °C) to constant weight.

Weather records (daily temperatures and solar radiation) were obtained from a meteorological station sited at 500 m from the experimental site. Daily incident PAR was obtained by multiplying solar radiation by 0.48 (Monteith, 1972). Photosynthetically active radiation (PAR) interception was registered every 10–15 days during each crop cycle. The fraction of intercepted PAR (*f_i*) was calculated as follows (Eq. (2)):

$$f_i = 1 - \frac{I_t}{I_0} \quad (2)$$

where, *I_t* is the incident radiation just below the lowest green layer of leaves and *I₀* is the incident radiation at the top of the canopy. The values for *I_t* and *I₀* were obtained with a linear 1 m-long PAR ceptometer (Cavadevices Bar-Rad, Arg.) horizontally and perpendicular to the rows. Five determinations per plot were made at each measurement date. PAR measurements were confined to the solar midday (1200–1300 h) on sunny days only. Daily fraction of PAR interception was obtained by linear interpolation within measurement dates. Daily incident PAR was multiplied by the corresponding daily fraction of PAR interception and accumulated

to obtain the total intercepted PAR by the crop. Mean radiation use efficiency (RUE) was calculated as the ratio between above-ground dry matter and intercepted PAR accumulated during the same period.

Grain yield was determined after grain black layer formation by hand harvesting all ears from a minimum area of 4 m² per plot. Harvest index (HI) was estimated as the ratio between grain yield and total aboveground dry matter at harvest. Final mean weight per grain was determined at harvest for each grain yield sample by weighting a 500 grains sub-sample. Aboveground dry matter, grain yield and mean weight per grain were expressed on a dry-weight basis (0% moisture content).

2.3.3. Crop growth rate and source-sink relationship

Actual and potential crop growth rate (CGR) were estimated for the EGFP. Actual CGR was estimated from dry matter measurements following Eq. (3). Potential CGR was performed by adapting the net canopy photosynthesis model of Monteith (1972). Monteith's adapted model was based on the daily incident PAR (Mj m⁻²), the measured daily fraction of intercepted PAR (*f_i*), and the potential RUE (g of aboveground dry matter per Mj of intercepted PAR) following Eq. (4). In Eqs. (3) and (4) *DM* indicates the aboveground

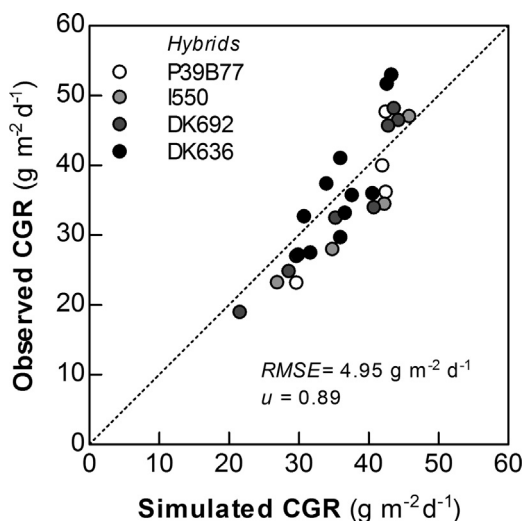


Fig. 1. Observed vs. simulated potential maize crop growth rates (CGR). Observed values were taken from well irrigated and fertilized maize crops at Balcarce (37° 45' S, 58° 18' W) during the period around 30 days bracketing silking. Data are from Exp. 2 and Exp.3 of present work (hybrids P39B77, I550 and DK692) and from sowing date maize experiments conducted by Cirilo and Andrade (1994a) (hybrid DK636). All these observed CGR data came from crops with near full interception (>95%) of photosynthetically active radiation. Root mean square error (RMSE) and Index of agreement (u) indicate simulation accuracy in absolute and relative terms, respectively.

dry matter in a specific moment, a and b indicate the beginning and the end of the EGFP, respectively and n indicates the length (in days) of the EGFP.

$$\text{Actual CGR (g m}^{-2}\text{d}^{-1}) = \frac{DM_b - DM_a}{n} \quad (3)$$

$$\text{Potential CGR (g m}^{-2}\text{d}^{-1}) = \frac{1}{n} \sum_a^b \text{PAR} \times f_i \times \text{RUE} \quad (4)$$

Potential RUE was estimated as a function of daily mean temperature (T_{mean}) according to Andrade et al. (1993) following Eq. (5). RUE estimations were confined to the range [6.7; 22.2] as lower and upper temperature limits, respectively, according to the temperature range used in CERES-Maize (López-Cedrón et al., 2005). Thus, for daily mean temperatures $\leq 6.7^\circ\text{C}$ or $\geq 22.2^\circ\text{C}$ constant values of 0 and 4.2 g MJ^{-1} were computed, respectively.

$$\text{RUE (g MJ}^{-1}) = 0.27 \times T_{\text{mean}} - 1.8 \quad (5)$$

The model was evaluated by comparing observed (O_i) vs. simulated (S_i) CGR values of crops growing under contrasting radiative and thermal conditions during the period of about 30 days bracketing silking (Fig. 1). Model accuracy was described using the root mean square error (RMSE) and the index of agreement (u) defined by Willmott (1981). RMSE was calculated following Eq. (6) and was used to describe the average error of simulations in absolute units ($\text{g m}^{-2} \text{d}^{-1}$).

$$\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^n (S_i - O_i)^2} \quad (6)$$

Index of agreement (u) was used to describe the model accuracy in relative units and was calculated as follows (Eq. (7)):

$$u = 1 - \frac{\sum_{i=1}^n (S_i - O_i)^2}{\sum_{i=1}^n (|S_i| + |O_i|)^2} \quad (7)$$

$|S_i|$ and $|O_i|$ indicate the absolute distance between S_i and \bar{O} , and between O_i and \bar{O} , respectively. This coefficient can take values from 0 to 1 indicating the degree to which the observed data is accurately estimated by simulation (a value of 1 indicates a perfect agreement and a value of 0 a complete disagreement between observed and simulated CGR).

An approximation to the source-sink relationship during the EGFP was performed for treatments of Exp. 3. To enable the comparison among treatments that differed in the length EGFP, values of source capacity and sink strength were expressed in a daily rate basis ($\text{g m}^{-2} \text{d}^{-1}$). Sink strength was calculated as the mean grain growth rate (GGR) by multiplying the mean growth rate per grain during the EGFP by the number of grains per unit area at harvest. Source capacity was based on the potential CGR for the same period. This methodological approach was carried out to avoid the potential autocorrelation between source and sink estimations caused by the negative feedback of an insufficient sink demand on photosynthesis (Paul and Foyer, 2001).

2.4. Data analysis

Data were analyzed through descriptive statistics, regressions and ANOVA procedures using the R statistical software (RDC Team, 2008). Lineal model for Exp. 1 and Exp. 2 was as follows (Eq. (8), adapted from Kuehl (2000)):

$$y_{ij} = \mu + \tau_i + \rho_j + e_{ij} \quad (8)$$

where y_{ij} is the observed response of the variable in the i^{th} -sowing date and j^{th} -block, μ is the general mean, τ_i is the effect of sowing date, ρ_j is the mean of the j^{th} -block deviation from the general mean and e_{ij} is the experimental error. Lineal model for Exp. 3 was as follows (Eq. (9)):

$$y_{ijk} = \mu + \alpha_i + \rho_k + d_{ik} + \beta_j + (\alpha\beta)_{ij} + e_{ijk} \quad (9)$$

where y_{ijk} is the observed response of the variable in the i^{th} -sowing date of the j^{th} -hybrid located in the k^{th} -block, μ is the general mean, α_i is the sowing date effect, ρ_k is the mean of the k^{th} -block deviation from the general mean, d_{ik} is the experimental error of the main plot, β_j is the hybrid effect, $(\alpha\beta)_{ij}$ is the interaction effect between sowing date and hybrid and e_{ijk} is the experimental error of the subplot. Sowing dates and hybrids were always considered as fixed effects. Additivity was assumed for all lineal effects. Appropriate standard errors according to Kuehl (2000) were calculated from residual sum of squares of each ANOVA. Estimated parameters were compared using t -tests ($\alpha = 0.05$).

3. Results

3.1. Meteorological conditions and crop development

The occurrence of crop phenological stages along the cropping seasons is shown in Fig. 2. The length of the sowing-emergence period was between 10–12 d for October, 7–9 d for November and 4–6 d for December and January sowing dates, in all experiments. Crops developed from mid-October to late April covering a broad range of thermal and radiative conditions. Frost free periods were 187, 187 and 169 days long for 2009–10; 2010–11 and 2011–12 seasons, respectively.

Frost events that occurred early in the cropping seasons during Exp. 2 and Exp. 3 damaged the leaves of October sowing dates (Fig. 2), affecting PAR interception only temporarily. Frost events that occurred late in the cropping season determined the cessation of crop growth during the reproductive period for most December and January sowing dates. These autumn frosts essentially acted as

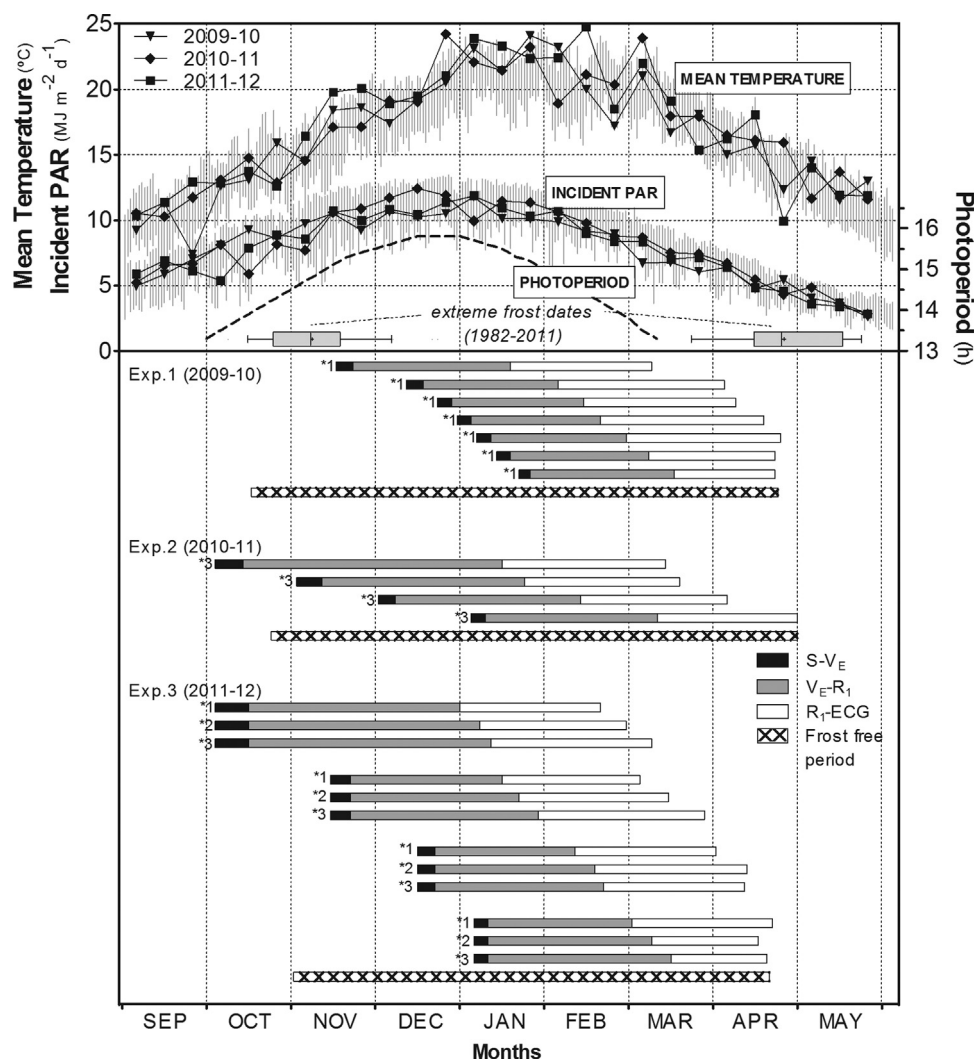


Fig. 2. Time-course of mean air temperature, incident photosynthetically active radiation (PAR) and photoperiod during maize cropping season at Balcarce ($37^{\circ} 45' S$, $58^{\circ} 18' W$). Vertical grey lines for temperature and PAR indicate the interquartile distance (i.e. the range between the 25th and 75th percentiles) of daily meteorological data (1982–2011 period). Boxes represent the length of maize phenological periods from sowing to emergence (S-V_E), emergence to silking (V_E-R₁) and silking to the end of crop growth moment (R₁-ECG). Left side numbers in each box indicate different hybrids (*1 for P39B77, *2 for I550 and *3 for DK692). Cross marked boxes indicate frost-free periods for each cropping season obtained from empirical observation in the field. Recorded minimum temperature in the weather station (at 1.5 m in the meteorological shelter) varied from 2.8 to 3.4 °C for each frost event in the field. Boxplot diagrams indicate the distribution of extreme frost dates for each year in the period 1982–2011 (daily minimum temperature <3 °C).

a defoliation since leaves died and grain filling continued, probably at the expense of sugar translocation from stems.

Average values of daily mean temperature and solar radiation during the reproductive period of each sowing date treatment were plotted together with those corresponding to representative maize systems of contrasting environments around the world (Fig. 3). Average values of early sowing dates of maize at Balcarce resemble those at temperate and high productive maize regions whereas, the average values of late sowing dates at Balcarce were similar to those at cool-temperate and less productive maize regions.

Table 1 shows the duration of the main phenological phases for each crop. The length of the EGFP (not directly shown in Table 1) can be calculated by subtracting the length of the “lag phase” to the silking-physiological maturity period. Duration of the lag phase varied as a function of the flowering time and lasted 10, 13 and 15 days when crops flowered during January, February and March, respectively. The emergence-silking period expressed in days was progressively reduced with the delay in sowing date but it was relatively constant for each hybrid when expressed in TT units (Table 1). Total cycle length (in days) differed among hybrids and was related

to the duration of the emergence-silking ($p < 0.001$; $R^2 = 0.82$) and silking-physiological maturity periods ($p = 0.002$; $R^2 = 0.37$). The length of the emergence-silking period expressed in TT units was related to the final number of leaves ($p < 0.001$; $R^2 = 0.87$) (Table 1). With the exceptions of treatments in which the grain filling period was prematurely interrupted, time (in days) from silking to physiological maturity of late sowings was similar or longer than that of early sowings (Table 1). Changes in sowing date exposed the photoperiod-sensitive stages of maize (estimated to be from V₄ to V₆) to contrasting photoperiods (Fig. 2) which ranged from around 13.9–15.8 h d⁻¹. Despite differences in the number of leaves in response to photoperiod (Table 1), TT from emergence to silking was not significantly affected by sowing date ($p > 0.34$).

3.2. Grain yield components and crop growth determining factors

Grain yields ranged from 1680 to 203 g m⁻² and were significantly affected by hybrid and sowing date (Table 2). Grain yields were directly associated with hybrid cycle length for October and November sowings (Exp. 3; $p < 0.001$; $R^2 = 0.86$). This positive

Table 2
Grain yield components and crop growth determining factors of contrasting maturity maize hybrids at different sowing dates in Balcarce (37° 45' S, 58° 18' W).

Exp.	Sowing Date	Hybrid	Grain Yield g m ⁻²	Grain number at harvest GN m ⁻²	Mean weight per grain at harvest mg	Emergence to silking period			Silking to ECG period			Harvest index	
						Accumulated incident PAR Mj m ⁻²	Mean fraction of PAR interception	RUE g Mj ⁻¹	Accumulated incident PAR Mj m ⁻²	Mean fraction of PAR interception	RUE g Mj ⁻¹		
1 (2009–10)	Nov-16	P39B77	1089	4313	253	599	0.41	–	464	0.88	–	0.53	
	Dec-11	P39B77	1019	3974	256	510	0.32	–	461	0.87	–	0.55	
	Dec-22	P39B77	904	3457	261	495	0.46	–	401	0.86	–	0.47	
	Dec-29	P39B77	759	3398	223	483	0.46	–	393	0.90	–	0.44	
	Jan-5	P39B77	608	3301	184	475	0.48	–	349	0.92	–	0.39	
	Jan-12	P39B77	417	3059	136	458	0.48	–	281	0.94	–	0.32	
	Jan-20	P39B77	203	2773	73	452	0.49	–	214	0.94	–	0.19	
		Sowing date			*	***	***	***	***	***	***	–	***
				(867)	(15)	(11)	(0.03)		(9)	(0.03)		(0.02)	
2 (2010–11)	Oct-4	DK692	1680	6522	258	918	0.42	3.6	575	0.92	3.8	0.51	
	Nov-2	DK692	1498	6157	243	826	0.44	3.8	517	0.93	3.6	0.49	
	Dec-1	DK692	1368	4933	278	745	0.56	3.8	431	0.96	3.5	0.44	
	Jan-3	DK692	579	4376	132	633	0.56	3.5	338	0.95	2.7	0.29	
		Sowing date			***	***	***	***	NS	***	NS	**	***
				(536)	(9)	(26)	(0.05)		(14)	(0.5)		(0.01)	
3 (2011–12)	Oct-4	P39B77	1250	4682	267	744	0.29	3.5	544	0.94	2.7	0.55	
		I550	1350	5604	240	832	0.38	3.6	536	0.96	3.0	0.49	
		DK692	1490	5570	268	875	0.39	3.6	558	0.95	3.2	0.50	
	Nov-14	P39B77	1240	4866	254	590	0.46	3.5	492	0.95	2.9	0.50	
		I550	1320	6102	216	654	0.54	3.6	499	0.97	2.8	0.47	
		DK692	1440	5538	260	726	0.55	3.8	524	0.95	2.8	0.50	
	Dec-15	P39B77	1110	4583	242	561	0.35	5.0 ^a	414	0.94	2.8	0.49	
		I550	1120	5252	214	634	0.43	4.8 ^a	407	0.97	2.8	0.48	
		DK692	1100	5160	213	654	0.43	4.7 ^a	388	0.96	2.9	0.45	
	Jan-4	P39B77	770	4219	182	511	0.53	3.8	339	0.95	2.2	0.46	
		I550	720	4959	145	570	0.54	3.7	279	0.95	2.1	0.44	
		DK692	630	4361	144	623	0.58	3.7	226	0.95	2.0	0.36	
		Sowing date			***	***	***	***	***	NS	***	***	***
					(281)	***	***	(0.06)	(0.3)	***	NS	NS	(0.01)
		Hybrid			***	***	***	NS	***	NS	NS	***	***
				(190)	***	***	(0.03)	NS	***	NS	***	***	
	Sowing date × Hybrid			NS	***	***	NS	NS	NS	***	***	***	
				(14)	(22)	(15)	(0.4)	(0.02)					

ANOVA p-values: * p < 0.05, ** p < 0.01, *** p < 0.001.

NS: not significant.

LSD values for means comparison are shown in brackets.

^a These RUE values may be overestimated. A heavy storm damaged temporarily canopy structure of these crops at V₁₂–V₁₄ phenological stage (35 d after emergence). Consequently, some of the midday PAR interception measurements before silking did not adequately estimate real PAR interception.

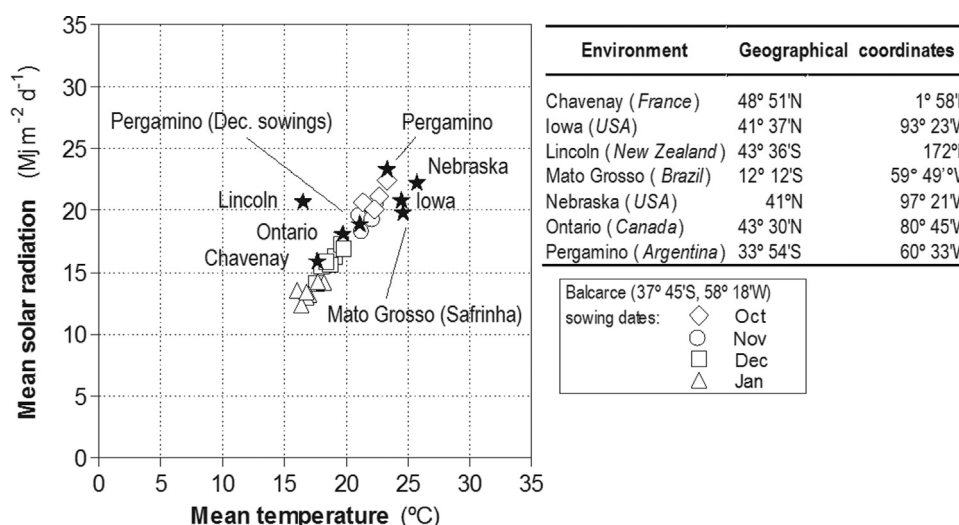


Fig. 3. Mean solar radiation and mean temperature from silking to physiological maturity of: i) maize crops sown at different sowing dates in Balcarce Exp. 1, Exp. 2 and Exp. 3 (empty symbols) and ii) representative maize crops of typical agricultural systems located in contrasting environments around the world (full star symbols). All these data correspond to temperate and cool temperate environment except Brazil. Safrinha cropping season in Mato Grosso (Brazil) involves delayed plantings that do not result in a deterioration of radiation and temperature during the reproductive period. Meteorological data were obtained from <http://power.larc.nasa.gov>.

relationship was reduced and even reversed as sowing date was delayed. Grain number per unit area was reduced proportionally less than weight per grain as sowing date was delayed.

The delay in sowing date reduced the amount of incident PAR from emergence to silking. Differences in the accumulated intercepted PAR during that period (not directly shown on Table 2), however, were smaller than those observed for incident PAR because of increases in the fraction of PAR interception as sowing date was delayed (Table 2, Fig. 4). Accumulated dry matter differed among hybrids in October and November sowings but only at the end of the crop cycle (Exp. 3; Fig. 4). Delaying sowing date reduced accumulated incident PAR by shortening the reproductive period (Table 1) and by placing this period toward the end of the season, when daily incident PAR had decreased (Fig. 2).

Harvest index decreased progressively with the delay in sowing date (Table 2). Grain yield was related to aboveground dry matter accumulated during the post-silking period ($p < 0.0001$; $R^2 = 0.94$). Thus, major changes in HI resulted from a disproportionate variation in the post-silking dry matter accumulation.

Since crops reached and maintained similar fractions of PAR interception after silking (Table 2), variations in the aboveground dry matter accumulated during the post-silking period resulted from differences in RUE and in accumulated incident PAR (Table 2) (multiple regression analysis $p < 0.0001$; $R^2 = 0.99$). Radiation use efficiency was positively associated with mean temperature ($p < 0.0001$; $R^2 = 0.32$) and, within each crop, RUE was lower during the post-silking vs. the pre-silking periods. Variation in RUE during the post-silking period was mainly accounted for by sowing date and differed among hybrids only for the October sowing date (Exp. 3, Table 2).

Actual post-silking dry matter accumulation was tested against a set of candidate variables (Table 3). The purpose of this analysis was to find predictor variables for the observed variation in grain yields. With the exception of time from silking to physiological maturity, all the evaluated variables showed a significant association with the target variable (Table 3). The most significant association was observed for potential post silking dry matter, which results from the product of the mean potential CGR and the time from silking to ECG.

The potential post silking dry matter values were then compared with the observed grain yields across all the experiments (Fig. 5). Grain yields were, in general, lower than potential post-

Table 3

Set of candidate explanatory variables for actual post-silking dry-matter accumulation.

Variable	Significance	r^a
Potential post-silking dry-matter	$p < 0.0001$	0.95
Mean Potential CGR (S-ECG)	$p < 0.0001$	0.89
Mean incident PAR	$p < 0.0001$	0.87
Mean temperature	$p < 0.0001$	0.85
Harvest Index	$p < 0.001$	0.70
Time from silking to ECG	$p < 0.001$	0.65
Photo-thermal quotient ^b	$p < 0.01$	0.63
Time from silking to Phys. Mat.	$p < 0.46$	0.16

^a Simple correlation coefficient of the variable with actual dry matter accumulation during the post-silking period.

^b Calculated as the quotient between average mean PAR and mean temperature during the period from silking to ECG.

silking dry matter. However, as sowing date was delayed, grain yields approached these estimated dry matter values (see 1:1 line and calculated RMSE and u for sowing dates prior and after Nov-15 in Fig. 5).

3.3. Source-sink relationships

The source-sink relationships during the EGFP are shown in Fig. 6. The variation of potential source capacity was higher than that of sink strength (Fig. 6a) and the source/sink ratio decreased from early to late sowing dates. In late sowings, the sink strength was higher than the potential source capacity (Fig. 6a). Actual and potential source capacity were similar only at late sowings (Fig. 6b). In early sowings, actual source capacity was lower than its corresponding potential source capacity and, to some extent, it was related to its sink strength.

4. Discussion

This work reappraised the effect of sowing date on maize grain yield and its components. The experimental set up at Balcarce provided a range of temperature and radiative conditions as wide as that found across temperate and cool-temperate maize environments (Fig. 3). The results of this work and the innovative approach to describe source-sink relationships can contribute to a better

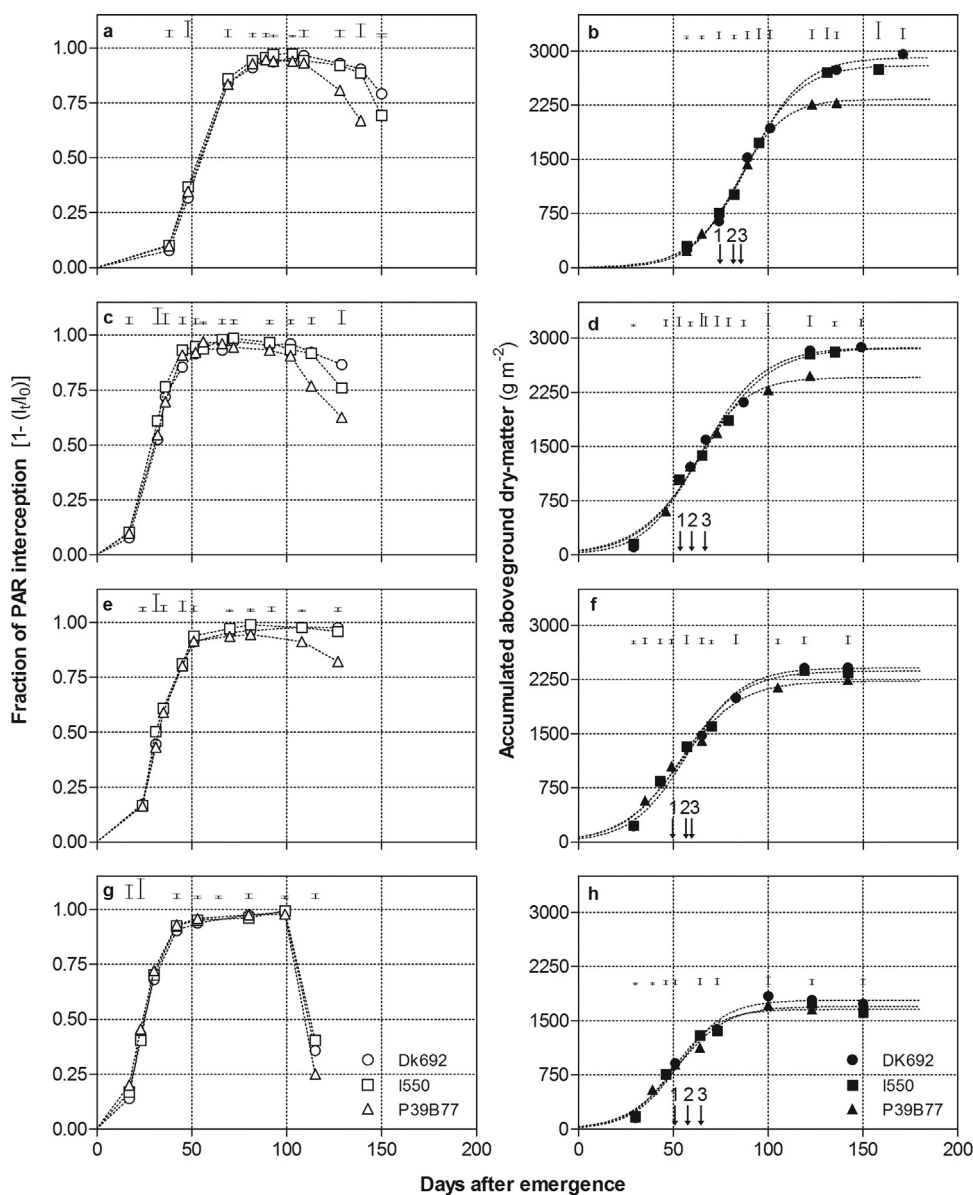


Fig. 4. Canopy fraction of photosynthetically active radiation (PAR) interception and accumulated aboveground dry matter as a function of time after emergence for October (a, b), November (c, d), December (e, f) and January (g, h) sowing dates of three maize hybrids: DK692, I550 and P39B77. Data from Exp. 3 (2011–12 growing season at Balcarce 37° 45' S, 58° 18' W). Arrows in graphs b, d, f and h indicate silking date for P39B77 (1), I550 (2) and DK692 (3). Vertical bars indicate the standard error of mean.

understanding of the effects of photo-thermal environmental conditions on maize grain yield determination.

4.1. Grain yield components and source-sink relationships

The reduction in number of grains per unit area was proportionally lower than that in weight per grain as sowing date was delayed. In contrast, previous studies (Cirilo and Andrade, 1994a,b) indicated that grain number reduction was the main cause of grain yield decreases with the delay in sowing date. Recent investigations evidenced that breeding efforts have steadily risen maize grain yield mainly through increases in reproductive sink strength. Thus, final weight per grain in current hybrids have become more prone to be source limited during the grain filling period (Cerrudo et al., 2013; Echarte et al., 2006).

As sowing date was delayed, crops maintained a relatively high number of grains per unit area (Table 2) with a growth rate (GGR) that exceeded their respective potential source capacity during the

EGFP (Fig. 6a). Grain growth of these source limited crops was not necessarily limited by assimilate availability since, in maize, sugar remobilization from the stem can contribute to grain filling (Daynard et al., 1969). The herein proposed source-sink analysis estimates net plant dry-matter stocks and does not consider internal translocation of assimilates. Hence, not all these source limited crops would increase grain yields in response to increases in assimilate availability. The method for assessing potential source capacity (Eqs. (4) and (5)) may also overestimate crop growth capability since it does not consider the progressive deterioration of canopy photosynthetic capacity during the grain filling period caused by leaf aging and senescence processes (Crafts-Brandner and Ponleit, 1987; Dwyer and Stewart, 1986). Despite these concerns, the method for assessing potential source capacity is useful since it provides a simple and robust estimation of the upper threshold of CGR. From this reference value, assimilate limitations to crop growth during the EGFP are promptly evident.

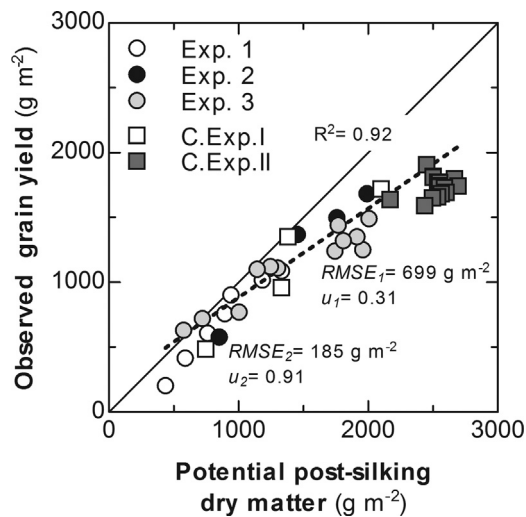


Fig. 5. Observed maize grain yield in relation to the simulated potential above-ground dry matter accumulated during the post-silking period. Simulation based on the potential crop growth rate (CGR) and the length of the reproductive period (time from silking to the end of crop growth (ECG)). Potential CGRs were calculated from daily incident PAR and mean temperature. Data of five maize experiments conducted at Balcarce ($37^{\circ} 45' S$, $58^{\circ} 18' W$) during 2009–10 (Exp.1), 2010–11 (Exp. 2), 2011–12 (Exp.3 and C. Exp. I) and 2012–13 (C. Exp. I) growing seasons. Root mean square error (RMSE) and index of agreement (u) are indicated for sowing dates prior Nov-15 (RMSE₁ and u_1) and after Nov-15 (RMSE₂ and u_2).

4.2. Radiation use efficiency

An interesting question arises from the observed RUE in Exp. 3 (Table 2): why did hybrids, with similar pre-silking RUE, differ in their post-silking RUE at early sowing dates but not at late sowing dates? Sink limitations can restrict photosynthesis when plants cannot allocate the photoassimilate production (Paul and Foyer, 2001). As shown in Table 2, hybrids with contrasting RUE during the post-silking period also differed significantly in their grain number per unit area. Hence, a possible hypothesis is that RUE differences among hybrids resulted from contrasting reproductive sink limitations during the grain filling period. The progressive reduction in radiation and temperature during the reproductive period as sowing date was delayed, turned the source more limiting than the sink for crop growth (Fig. 6a). When the source capacity became the limiting factor, crop growth was independent of the sink strength and all hybrids showed similar post-silking RUE.

The analysis of RUE revealed that the different current hybrids had similar canopy photosynthesis capability. Moreover, pre-silking RUE values did not differ from those observed by Andrade et al. (1993) for older hybrids. These observations are consistent with those reported by Tollenaar and Aguilera (1992) who studied hybrids from different breeding eras and found RUE differences only for the post-silking period, during which, contrasting sink limitations among hybrids were manifested. Sink limitations of early sown maize can be reduced or removed through increases in plant density (Sarlangue et al., 2007). Conversely, grain yield responses to increases in plant density would not be expected to occur in any case when source capacity is the limiting factor (e.g. late sowing dates), except for situations where crop canopy does not reach full PAR interception.

4.3. Harvest index and modelling approaches

Delaying sowing resulted in similar (or slightly increased) amounts of dry matter at silking (Fig. 4), indicating that dry matter allocation to vegetative structures was practically unchanged by sowing date. In contrast, for the post-silking period, shorter

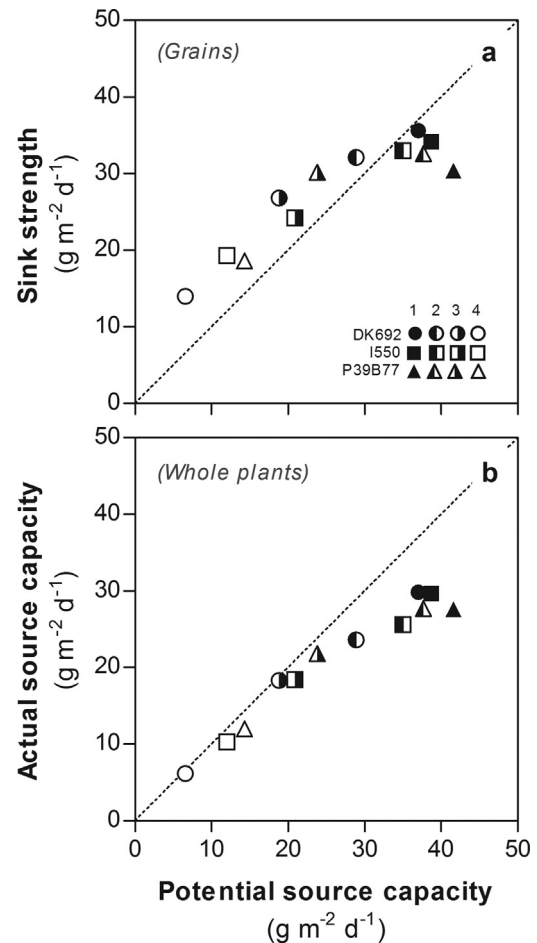


Fig. 6. Source-sink relationship during the effective grain filling period (EGFP) of maize in Balcarce ($37^{\circ} 45' S$, $58^{\circ} 18' W$) as affected by four contrasting sowing dates (Oct-4 (1); Nov-14 (2); Dec-15 (3); Jan-4 (4)) and three contrasting maturity hybrids (DK692, I550 and P39B77). Observed sink strength in relation to the potential source capacity (a) and actual source capacity in relation to the potential source capacity (b). Sink strength is indicated as the mean grain growth rate (GGR) during the EGFP expressed on a community basis ($g m^{-2} d^{-1}$). Source capacity (both potential and observed) is indicated as the mean crop growth rate (CGR) during the EGFP. Dotted line in both graphs indicates 1:1 relation. Data from Exp. 3, see material and methods for details about estimations of GGR and potential and actual CGR.

durations and lower CGRs in late vs. early sowing dates reduced markedly the dry matter allocated to grains. These unbalanced changes in dry matter accumulation explained the observed variation in HI. Previous investigations in maize (Maddoni, 2012; Otegui et al., 1996) carried out grain yield simulations by multiplying an estimated aboveground dry matter (accumulated between emergence and physiological maturity) by a fixed value of HI = 0.46. A similar modelling approach was also proposed by Muchow et al. (1990) but including a model algorithm that progressively modified the HI as a function of grain development.

The present work not only evidenced an inconsistency in using a constant value of HI, but also, found a simple alternative to simulate the effect of sowing date on maize grain yield (Fig. 5). This modeling approach can be useful, for example, to assess the relevance of the grain yield interaction between sowing date and hybrid cycle length (Exp. 3; Table 2). The most suitable combination of hybrid maturity class and sowing date depends mainly on the length of the cropping season (Olson and Sander, 1988; Shaw, 1988) and, for any particular environment, its assessment requires an analysis based on a long term series of climate data. It should be noticed that a simulation model based on the potential post-silking dry matter accumulation assumes by definition that grain yield is

source-limited. This implies that reproductive sink strength does not limit the photoassimilate allocation to grains during the post-silking period. Accordingly, as shown in Figs. 5 and 6, observed grain yields would approach simulated potential post-silking dry-matter as long as the sink strength reaches or exceeds the source capacity.

4.4. Agronomic prospects

Late sowings of maize have become a frequent practice in rainfed systems of Argentina. Farmers have implemented this practice to reduce the risk of water deficit during the critical flowering period (Maddonna, 2012) despite the deterioration of environmental conditions (radiation and temperature) for crop growth during the reproductive period. Maize grain yield in delayed sowings is less variable across years and closer to its corresponding potential grain yield when compared with that of early sowings (Mercau et al., 2014). Hence, some agronomic prospects can be derived from our results to the management strategies for late sown maize of rainfed systems.

Crop growth during the EGFP of late sown maize was limited by photosynthetic source capacity because actual grain growth rate exceeded the potential crop growth rate (Fig. 6a). This extra grain growth had to be supported by remobilization of carbohydrates (Daynard et al., 1969; Uhart and Andrade, 1991). Hence, for late sowings, farmers must take into account the root and the stem strength of hybrids to avoid agronomic difficulties associated with lodging and stem breakage.

In addition, the source limitation in late sown maize indicates that the physiological condition of maize plants during the grain filling period has become as relevant as the critical flowering period. Thus, those recommendations based on the optimization of the crop physiological condition around flowering (Andrade et al., 2005) should be reviewed for late sowings of current maize hybrids. Our results suggest that crop management for late sown maize needs to be focused, also, in preserving optimal physiological conditions for crop growth during the grain filling period.

5. Conclusions

Based on the progressive deterioration of the photo-thermal conditions for maize growth during the last part of the cropping season, this work attempted to elucidate the factors that limit grain yields when sowing date is delayed. We explored a broad range of sowing dates in a temperate maize region where solar radiation and temperature vary widely along the cropping season. A consistent response of grain yield components and source-sink relationships indicated that, as sowing date is delayed, the supply of assimilates to grains (source capacity) becomes more limiting than the demand for assimilates by grains (sink strength) during the grain filling period. These results prompt further research to review strategies and recommendations for late sown maize.

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