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Eco-physiological changes in sorghum hybrids released in Argentina over the last 30 years

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ABSTRACT

The development of single-cross hybrids during mid-1950s was important for sorghum [*Sorghum bicolor* (L.) Moench] improvement worldwide. Within the hybrid era, however, there is limited information on sorghum genetic progress. Our main objective was to evaluate the genetic gain for grain yield and other phenotypic traits for grain sorghum commercial hybrids released in Argentina from 1984 to 2014. A second objective was to describe common attributes behind high-yielding hybrids. A total of 43 hybrids were grown at three different environments. Evaluated traits were grain yield, yield components (grain number m^{-2} and individual grain weight), phenology, plant height, stay-green, crop growth rate around flowering, reproductive biomass partitioning, grain set efficiency, biomass at maturity, harvest index and post-anthesis source/sink ratio.

Yield across environments varied from 8.1 to 10.8 t ha^{-1}. Genetic progress for grain yield was 8.7 ± 2.9 kg ha^{-1} $year^{-1}$ ($p < 0.01$) across environments. This progress represented only 0.1% of the experiments mean grain yield. Modern hybrids set more grains per unit of reproductive biomass ($p < 0.10$), have more stay-green ($p < 0.10$), and showed higher post-anthesis source/sink ratio ($p < 0.10$) when compared to older ones. By clustering hybrids irrespective of the year of market release, three groups were conformed showing important grain yield differences. Common traits among high-yielding hybrids were high grain number, low grain size, later flowering time, intermediate height and stay-green trait. Within the high-yielding cluster, hybrids showed significant variability in crop growth rate around flowering, biomass at maturity, reproductive biomass partitioning, grain set efficiency, harvest index and post-anthesis source/sink ratio that could be exploited in breeding programs, describing opportunities for sorghum improvement in temperate environments.

1. Introduction

Sorghum is the fifth most important cereal crop in the world. In 2013 the global average sorghum yield was 1.45 t ha^{-1} (FAO, 2014). This low yield is mainly attributed to growing the crop in environments with large biotic and abiotic stresses. In Argentina the average yield in 2013 was 4 t ha^{-1} of a total harvested area of 900,000 ha (FAO, 2014). Improving our understanding of sorghum grain yield determination is relevant for future breeding strategies (Richards et al., 2001; Araus et al., 2008) as the crop has competitive important advantages. They include high biomass production, grain quality and yield stability in adverse conditions due to the inherent drought and high temperature tolerance.

For grain sorghum the most important selection criteria used by breeders are direct measurements of grain yield and grain yield stability. Selection is commonly based on performance trials across a wide number of sites and years. The ultimate goal is a fast release of better hybrids into the market (Duvick and Cassman, 1999). Other possible selection criteria are indirect measurements based on phenotypic traits associated with grain yield. Desirable traits must have high heritability, and need to be relatively easy to select in order to generate rapid progress in breeding programs (Richards et al., 2001). In these sense, retrospective studies are extensively used as a key tool to guide and assist crop improvement (Duvick, 2004; Pask and Reynolds, 2013).

Retrospective studies consist on evaluating genetic gain for yield and associated traits in a range of genotypes released to the market during a defined time period. Genotypes are grown simultaneously

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Abbreviations: CGR, crop growth rate around anthesis; P_R, reproductive biomass partitioning; E_G, grain set efficiency; Post-anthesis S/S ratio, post-anthesis source/sink ratio; Exps, experiments; BLUPs, best linear unbiased predictors; BLUEs, best linear unbiased estimators; OLS, ordinary least squares; PCA, principal component analysis.

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Table 1
General description of the three Experiments (Exp).

Exp	Year	Planting date	N at sowing[a] (kg ha^{-1})	N applied (kg ha^{-1})	Plant density (pl m^{-2})	Irrigation
I	2014	Nov 13	24	200	20	Yes
II	2013	Nov 3	16	100	20	No
III	2014	Nov 12	16	0	30	No

[a] 0–60 cm depth.

under equal environment and management conditions (Calderini et al., 1999). Although several limitations to these studies have been recognized (e.g., it does not take into account management and climate variation interactions with the hybrid effect; Bell et al., 1995; Calderini et al., 1999), they allow the measurement of specific traits that could be difficult to phenotype in wider-scale studies. The analysis of historical multi-environmental trials (METs) from a particular breeding program covers these limitations (de la Vega et al., 2007a) and, when available, can complement retrospective studies (Piepho et al., 2014).

Detailed retrospective breeding studies in sorghum are scarce. Blum et al. (1991) showed that grain yield improvement in open-pollinated sorghum cultivars was three to four fold higher than landraces. This gain was attributed to a reduction in plant height and a harvest index increase. From 1950 to 1980, modern hybrids in the USA exhibited 39% more grain yield than older ones (Miller and Kebede, 1984). Contrary, this was a consequence of plant height, biomass and leaf area increases (Miller and Kebede, 1984). There is no available information testing modern materials under temperate environments.

Genetic gain depends on the environmental quality. Studies in maize are suggesting yield increases are higher in more stressful environments thought the improvement of defensive traits (Duvick and Cassman, 1999). A study in sorghum in USA showed that grain yield under rainfed conditions has increased 46 kg ha^{-1} year^{-1} from 1957 to 2008, while grain yield under irrigated conditions has remained unchanged (Assefa and Staggenborg, 2010). A similar trend was observed in sunflower (López Pereira et al., 1999). This differential response highlights the importance of exploring a range of environments. Because sorghum hybrids are commonly grown for broad adaptation, computing the genetic progress across environments is also particularly important (de la Vega et al., 2007a).

The main objective of our study was to quantify the genetic gain for grain yield and associated phenotypic traits in grain sorghum hybrids released in Argentina from 1984 to 2014. Forty-three commercially representative hybrids were grown under three different environments. A second objective explored eco-physiological attributes behind high yielding hybrids.

2. Materials and methods

2.1. Plant material and experimental design

Field experiments were conducted during 2012–2013 and 2013–2014 growing seasons (from now-on referred as 2013 and 2014) at the Campo Experimental Villarino, Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, at Zavalla (33° 1′ S, 60° 53′ W, 130 m altitude), Santa Fe Province, Argentina. The soil type was a silty clay loam Vertic Argiudoll (Soil Taxonomy, Soil Survey Staff 2014). A total of three experiments (Exps) were conducted to generate three different environmental conditions (Table 1). Exps I and III were conducted in 2014 and Exp II was conducted in 2013 (Table 1). Fertilization, water availability and stand density varied at each particular environment (Table 1).

The experimental design at each experiment was a randomized complete block with three replicates. Plots were four rows 5.5 m long with 0.52 m row spacing. Plots were over-sown and thinned after emergence to the target stand density (Table 1).

Soil samples (0–60 cm) were taken before sowing and analyzed for P (0–20 cm) and N-NO$_3$ (0–60 cm). Nitrogen (UREA) was applied at V4–V5 stage (Vanderlip and Reeves, 1972) to reach different fertilization levels depending on the particular experiment (Table 1). Additionally, MAP was applied at sowing at a rate of 150 kg ha^{-1} in Exps I and II. Diseases were controlled by weekly fungicide applications during the flowering period. Irrigation was applied with a sprinkler irrigation system based on visual plot observations and weather forecast.

A total of 43 hybrids were tested. Hybrids were released in Argentina from 1984 to 2014 and were commercially representative at the country level. Two hybrids were pre-commercial (V82226 and V80435) from the Advanta Semillas sorghum testing program. Due to seed limitations not all hybrids were tested in all environments; where 28, 34 and 40 hybrids were tested in Exps I, II and III, respectively (Table 2). Hybrids are medium maturity, with the exception of GR80 and ADV114 (short maturity) and VDH422 (late maturity). All hybrids are grain sorghum hybrids. Hybrid VDH422 is a dual purpose sorghum that is grown for both stover and grain production.

2.2. Phenotypic traits

Anthesis was recorded when 50% of the plants in each plot had at least one visible anther. Physiological maturity was recorded after visual observations of black layer in five of ten consecutive plants at basal panicle positions (van Oosterom and Hammer, 2008). Time to anthesis and grain filling duration (anthesis to maturity) was computed in thermal time. A base temperature of 11 °C was used before anthesis and 5.7 °C after anthesis (Hammer et al., 1993; Heiniger et al., 1993).

Above-ground biomass samples were obtained after cutting one square meter of total above-ground biomass per plot at ~20 days before anthesis and 10 days after anthesis (Pepper and Prine, 1972; van Oosterom and Hammer, 2008; Gambín et al., 2008). Shoot biomass was always measured after drying plants in an air-forced oven at 65 °C for at least one week. Panicle biomass at the pre-anthesis sample was assumed to be zero. Panicle biomass at the post-anthesis sample was weighted separately. Panicles were always cut one centimeter below the first primary branch (being fertile or not). Tillers were treated like main stem. At physiological maturity two square meters of panicles were harvested per plot. Panicles were dried and threshed, and the number of grains and individual mean grain weight were estimated from the weight of an aliquot of 200 grains.

Crop growth rate around anthesis (CGR) was calculated as the ratio between the accumulated aboveground biomass (g m^{-2}) from pre- to post-anthesis biomass samples and the thermal time between stages. Biomass partitioning to the panicle (P_R) was calculated as the ratio between the post-anthesis reproductive biomass and CGR. Grain set efficiency (E_G) was calculated as the ratio between grain number (m^{-2}) and post-anthesis panicle biomass (g m^{-2}) following Gambín and Borrás (2013). Post-anthesis source/sink ratio was calculated as the ratio between the

Table 2
List of hybrids tested at each Experiment (Exp), together with the market release year for each hybrid.

Hybrid	Year of release	Exp		
		I	II	III
GR80	1984	x	x	x
MAXIMO	1984	x	x	x
ACA550	1988	x	x	x
ARRIERO	1988	x	x	x
ACA557	1988	x	x	x
BERMEJOG140	1991		x	x
A9904	1991	x	x	x
FRONTERIZO	1993	x	x	x
NATIVO	1993		x	
ALFA	1993		x	x
Lider 140	1993	x		x
TELEN	1994	x	x	x
8419	1995	x	x	x
BUSTER	1996	x	x	x
81G29	1998		x	x
VDH302	1998		x	x
ACA558	1998	x	x	x
DK52 ARG	2001		x	x
VDH203	2001		x	x
84G62	2002	x	x	x
MS 108	2002	x	x	x
VDH303	2003		x	x
VDH422	2003		x	x
VDH314	2004	x	x	x
PAN 8816	2005	x	x	x
A9758M	2005	x		x
MS102	2006		x	x
TS281	2006	x	x	x
VDH206	2007		x	x
NK 240	2007	x	x	x
81T35	2008		x	
81G67	2008			x
VDH306	2009	x	x	x
83G19	2010	x	x	x
ADV114	2010	x	x	x
V82226[a]	2012		x	
DK 53	2012	x		x
DK64T	2012	x		x
TS267	2012			x
TS283	2012	x		x
ADV1200	2013	x	x	x
V80435[a]	2014	x		x
A9770M	2014	x		x

[a] Pre-commercial hybrids from the sorghum testing program of Advanta Semillas.

accumulated total plant biomass from 10 days after anthesis to physiological maturity and grain number (mg grain^{-1}).

Final plant height (from ground level to the top of the panicle) was measured on five consecutive random plants per plot. Stay-green was estimated using a visual scale of 1–5 (1: fully green; 5: total senescence; Xu et al., 2000) at physiological maturity in each plot. Harvest index was computed as the quotient between grain yield and total plant biomass at physiological maturity (stover + grain).

Biomass samplings were not done in Exp I. For this reason, biomass at maturity, harvest index, CGR, P_R, E_G and post-anthesis source/sink ratio are not reported for this particular experiment.

2.3. Statistical analysis

Data were analyzed using linear mixed-effects models in R (R Core Team, 2014; version 3.0.2, lme4 package, lmer function) (Bates et al., 2014). For each trait best linear unbiased predictors (BLUPs) of the hybrid effects were computed. BLUPs give a proper estimate of the hybrid effect across different growing conditions, and were obtained following procedures described in de la Vega et al. (2007b).

First, best linear unbiased estimators (BLUEs) for grain yield were obtained fitting a mixed-effects model for each Exp separately. This model considered hybrid as fixed effect and block as random effects and was fitted using the restricted maximum likelihood method (Zuur et al., 2009). BLUEs calculated for each individual Exp was plotted against the year of hybrids release to explore genetic progress × environmental interaction. There was no model improvement after considering a genetic progress × environmental interaction (not shown) and for this reason data was analyzed jointly.

In the pooled analysis variance components for each trait were determined by fitting a linear mixed-effects model. In this model environment was considered a fixed effect while block within environment, hybrid and hybrid × environment interaction were considered random effects. The set of hybrids used in this study can be considered as a representative sample of the genetic commercial variability used in sorghum breeding in Argentina during the period analyzed. Parameter estimates for final model were obtained using the restricted maximum likelihood method (Zuur et al., 2009).

The BLUPs of the hybrid effects for each trait were plotted against the hybrids release year. Using all data points ordinary least squares (OLS) regressions were computed to estimate average genetic gain over time. As an estimate of the performance of "high-yielding hybrids", genetic gain estimates were computed as the slopes of fitted 0.90 quantile regressions, which are assumed to describe the upper boundaries of the hybrid trait BLUPs to year of release relationship (de la Vega and Chapman, 2010). Quantile regression was fitted in R (quantreg package, Koenker, 2013).

Hybrid by trait matrix of BLUPs was constructed for pattern analysis (de la Vega et al., 2007b). Two matrices were constructed separately for traits that were measured in all or two Exps. Matrices were centered within column through subtraction of the trait mean and normalized by division of the remainder by the within-column standard deviation. Normalization was necessary because traits had different scales. Classification employed a hierarchical agglomerative clustering method (Williams, 1976) with squared Euclidean distance as the dissimilarity measure, and incremental sum of squares (Ward, 1963) as the fusion criterion. A dendogram was constructed to investigate similarities in performance pattern among hybrids in terms of their relative responses for particular traits of interest (grain yield and traits with low hybrid x environmental interaction). The principal component of the squared Euclidean distance matrices of hybrids x traits were estimated using a singular value decomposition procedure and biplots of the first two components principals (PCs) were displayed for interpretation. Cluster analysis and principal components analysis (PCA) were done in R (cluster package; Maechler et al., 2014).

3. Results

3.1. Growing conditions

Total rainfall from sowing to physiological maturity was 525 and 716 mm in 2013 (Exp II) and 2014 (Exps I and III), respectively. In Exp I ca. 100 mm were added in three times during the pre-anthesis period (December and January), totalizing 816 mm. Minimum and maximum monthly air temperatures were similar between years, averaging 15.6 °C and 28.2 °C, respectively.

A large proportion of the total grain yield variance was attributed to the growing environment (47.5%; Table 3). Average grain yield was 8.1 t ha^{-1} in Exp III, 9.6 in Exp II and 10.8 t ha^{-1} in Exp I (Table 3). These results confirmed that managed growing conditions (through irrigation, N, and stand density) were successful for creating different environments.

Table 3

Average, minimum (Min) and maximum (Max) phenotypic values for traits analyzed in Exps I, II, and III. Variance components (in percentage) associated with environment (E), hybrid (H), HxE interaction, block nested within E and residual are described. Genetic progress was analyzed fitting a OLS regression analysis and 90 quantile regression on BLUPs of genotypic effects for each trait versus the year of commercial release.

Exp		Grain yield ($kg\,ha^{-1}$)	Grain number (m^2)	Grain weight ($mg\,grain^{-1}$)	Plant height (m)	Stay-green (score1–5)[a]	Time to anthesis (°Cd)	Duration of grain filling (°Cd)
I	Average	10869	38439	26	1.6	2.1	1107	877
	Min	8139	23879	19	1.2	1.8	954	747
	Max	13641	67808	34	2.0	2.5	1198	988
II	Average	9631	36359	25	1.4	1.9	928	788
	Min	7581	27281	19	1.1	1.2	791	576
	Max	12077	54874	30	1.8	2.5	1038	1033
III	Average	8123	32246	24	1.4	2.2	1046	863
	Min	7074	24106	17	1.1	1.7	905	736
	Max	9598	45196	29	2.0	2.7	1327	974
% Variance								
	E	47.5	13.1	14.7	40.0	12.9	66.5	24.2
	H	3.5	37.2	61.5	45.9	12.8	21.7	1.6
	HxE	10.5	5.3	2.8	5.8	8.4	4.2	23.0
	Block(E)	1.6	3.0	<1	<1	10.3	2.0	<1
	Residual	36.8	41.5	21.0	7.3	55.6	5.6	50.7
	HxE to H ratio	3.00	0.14	0.05	0.13	0.66	0.19	13.94
Genetic progress								
OLS regression (r)		$8.7 \pm 2.9^{**}$ (0.41)	ns	ns	ns	$-0.003 \pm 0.001^{\cdot}$ (0.22)	ns	ns
90 Quantile regression		ns	ns	ns	ns	$-0.006 \pm 0.003^{\cdot}$	ns	ns

$^{\cdot}$, *, **, *** significant at $p < 0.10$, 0.05, 0.01, and 0.001 respectively, ns: not significant.

[a] Stay-green score ranged from 1 (fully green) to 5 (total senescence).

Table 4

Average, minimum (Min) and maximum (Max) phenotypic values for traits analyzed at Exps II and III. Variance components (in percentage) associated with environment (E), hybrid (H), HxE interaction, block nested within E and residual are described. Genetic progress was analyzed fitting a OLS regression analysis and 90 quantile regression on BLUPs of genotypic effects for each trait versus the year of commercial release.

Exp		Biomass at maturity ($g\,m^{-2}$)	Harvest index	CGR[a] ($g\,m^{-2}\,°Cd^{-1}$)	P_R[b] ($°Cd^{-1}$)	E_G[c] ($grain\,g^{-1}$)	Post-anthesis S/S ratio[d] ($mg\,grain^{-1}$)
II	Average	2340	0.41	2.36	125	126	17
	Min	1995	0.33	1.71	95	96	7
	Max	2687	0.52	2.82	189	177	28
III	Average	2181	0.37	2.02	161	126	17
	Min	1928	0.32	1.52	90	64	5
	Max	2574	0.42	3.34	253	218	52
% VariancE							
	E	10.6	20.8	18.4	17.8	<1	<1
	H	2.2	9.3	8.5	6.1	11.1	1.7
	HxE	7.4	15.5	<1	8.1	<1	<1
	Block(E)	7.5	<1	<1	1.0	<1	9
	Residual	72.2	54.4	73.1	67.0	88.9	89.3
	HxE to H ratio	3.38	1.67	<1	1.31	<1	<1
Genetic progress							
OLS regression (r)		ns	ns	ns	ns	$0.31 \pm 0.16^{\cdot}$ (0.22)	$0.01 \pm 0.006^{\cdot}$ (0.22)
90 Quantile regression		ns	ns	ns	ns	ns	ns

$^{\cdot}$, *, **, *** significant at $p < 0.10$, 0.05, 0.01, and 0.001 respectively, ns: not significant.

[a] CGR: crop growth rate around anthesis.

[b] P_R: reproductive biomass partitioning.

[c] E_G: grain set efficiency.

[d] Post-anthesis source/sink ratio.

Time to anthesis and plant height were among the traits that varied the most across environments (>40%; Table 3). Percentage of variance associated with differences among environments was lower than 25% for the rest of the traits (Tables 3 and 4).

3.2. Genetic progress

Significant hybrid and hybrid × environmental interaction effects ($p < 0.05$) were found for most measured traits. For grain number per square meter, grain weight, time to anthesis, plant height and stay-green, hybrid-to-hybrid variation was larger than the hybrid × environment interaction (low HxE to H ratio; Table 3). The same applied for CGR, E_G and post-anthesis source/sink ratio, although the residual component for these particular traits was large (higher than 70%). The hybrid × environment interaction was more important than the hybrid effect for grain yield, grain filling duration, biomass at physiological maturity, harvest index and P_R (Tables 3 and 4).

There was no evidence of different rates of genetic progress for grain yield across the three environments tested, so data were analyzed jointly. Ordinary least squares regression analysis showed that grain yield increased linearly by $8.7 \pm 2.9\,kg\,ha^{-1}\,year^{-1}$ over the period from 1984 to 2014 (Fig. 1). Ordinary least squares regression represents the average performance. This rate repre-

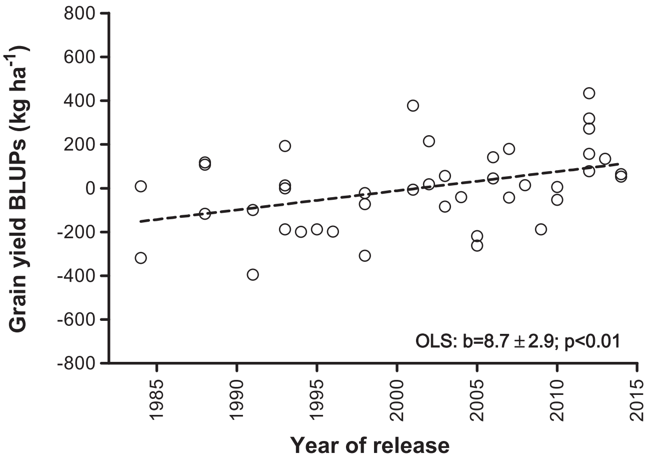

Fig. 1. Best linear unbiased predictors (BLUPs) for grain yield for a total of 43 hybrids against year of hybrid commercial release from 1984 to 2014.

sented a 0.1% relative to the average grain yield of the considered period. When analyzing the performance of high-yielding hybrids for the same period, computed as the slopes of 0.90 quantile regression, genetic gain estimates were not significant (Table 3). Across all measured traits genetic progress was negative for stay-green scores ($p < 0.10$), and positive for E_G ($p < 0.10$) and post-anthesis source/sink ratio ($p < 0.10$; Tables 3 and 4). However, when computing the 0.90 quantile regression the slope was significant only for stay-green ($p < 0.10$, Fig. 2a). Stay-green scores were lower in modern hybrids, showing modern hybrids retaining their green leaf area for a longer period than older ones.

3.3. Characteristics of high-yielding hybrids

Clustering according to the BLUPs of the hybrid effects for grain yield and traits with low HxE to H ratio (grain number, 1000 grain weight, plant height, stay-green and time to anthesis) allowed exploring the relationship between hybrids and traits, and associations among traits. This was of particular interest here as there was no clear genetic progress for most evaluated traits.

Clustering was truncated at the three group level (more than 50% of similarity retained, dendogram not shown). Groups 1, 2 and 3 were composed by 9, 21 and 13 hybrids, respectively (Table S1). Their corresponding hybrid release average for the different groups were 2002, 2001 and 2002 for groups 1, 2 and 3, respectively, showing that the classification was not related to the hybrid release year.

Group 1 exhibited the lowest average grain yield (Fig. 3a). They were also the shortest height hybrids, with reduced time to anthesis and stay-green (Fig. 3a–f). Group 2 was similar to group 1 in average yield, but grouped taller, non-stray-green and large individual grain weight hybrids. Group 3 grouped high-yielding hybrids, showing later flowering time, and intermediate plant height and stay-green (Fig. 3a–f). Hybrids within group 3 showed the highest grain number per square meter and the lowest individual grain weight (Fig. 3a–c).

Fig. 4 depicts a biplot simultaneously representing the relationships between hybrids and traits. Hybrids are shown by numbers representing the hybrid cluster groups (1, 2 or 3), and traits are represented with vectors. The seven-dimension trait BLUPs was reduced by PCA to two dimensions that explained 67% of the original information (Fig. 4). The diagram showed that grain yield was positively correlated with grain number and negatively with grain weight. Grain yield was partially correlated with time to anthesis and plant height, and showed no correlation with stay-green.

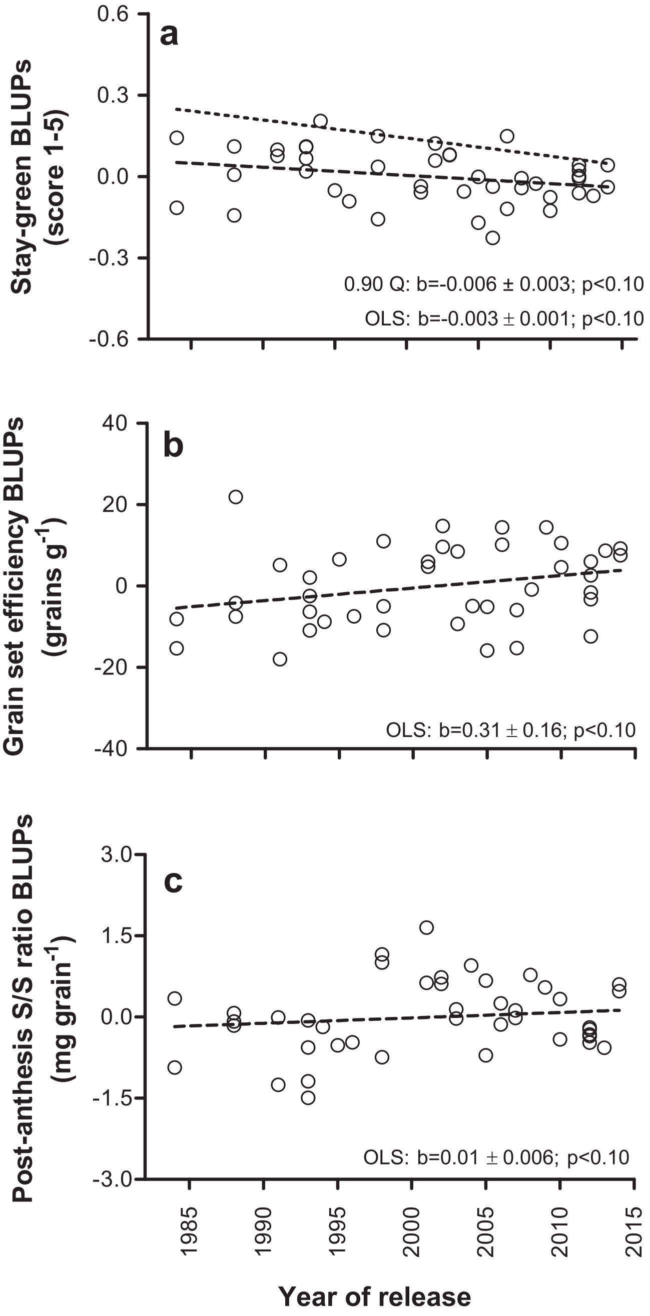

Fig. 2. Best linear unbiased predictors (BLUPs): (a) stay-green, (b) grain set efficiency, (c) post-anthesis source/sink ratio, for a total of 43 hybrids against year of hybrid commercial release from 1984 to 2014. Dashed and dotted lines are the ordinary least squares (OLS) and 0.90 quantile regression functions, respectively. Stay-green scores ranged from 1 (fully green) to 5 (total senescence).

Progressions from top-left to bottom-right in the biplot represent increasing grain yield and grain number, from bottom-right to top-left increases in grain weight and from top-right to bottom-left increases in time to anthesis, stay-green and plant height. Hybrids belonging to group 3 were localized at the right of the diagram, presenting the highest values for grain yield and grain number (Fig. 4). Group 2 was localized at the left of the diagram, presenting intermediate grain yield and highest grain weight values. Finally, hybrids belonging to group 1 were observed at the top of the diagram, having low grain yield, short plant height and time to anthesis (Fig. 4).

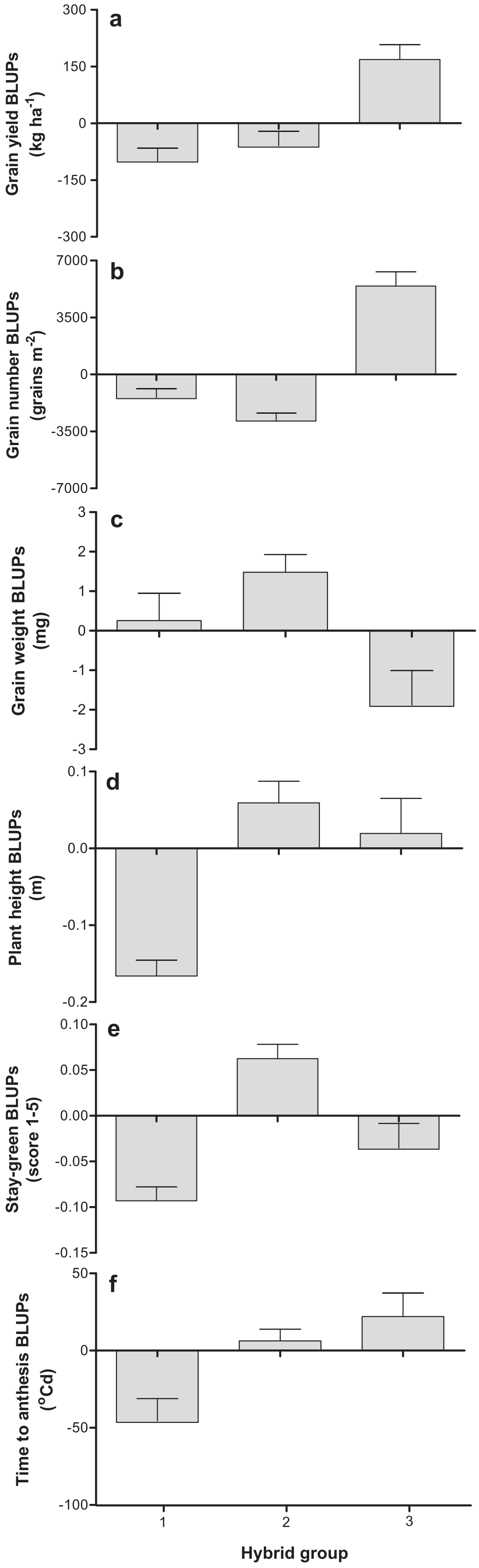

Fig. 3. Hybrid group best linear unbiased predictors (BLUPs) from hierarchical agglomerative cluster method of: (a) grain yield, (b) grain number, (c) grain weight, (d) plant height, (e) stay-green and (f) time to anthesis.

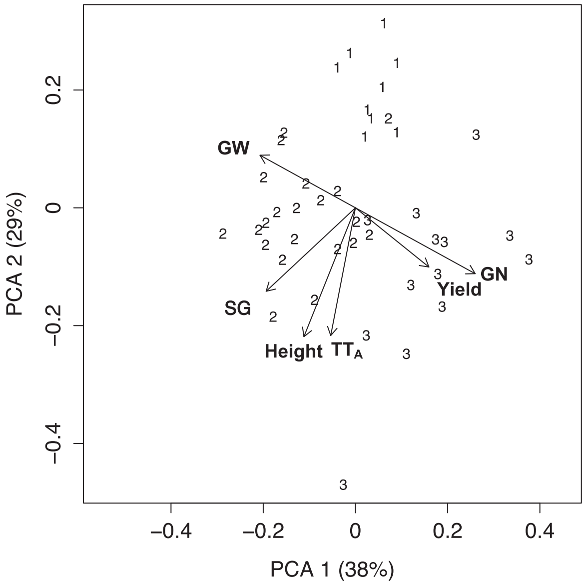

Fig. 4. Biplot of the first and second principal components based on the best linear unbiased predictor (BLUPs) for: grain yield (Yield), grain number (GN), grain weight (GW), plant height (Height), stay-green (SG) and time to anthesis (TT_A) for a total of 43 hybrids released from 1984 to 2014. Numbers indicate the three groups identified by hierarchical agglomerative cluster method.

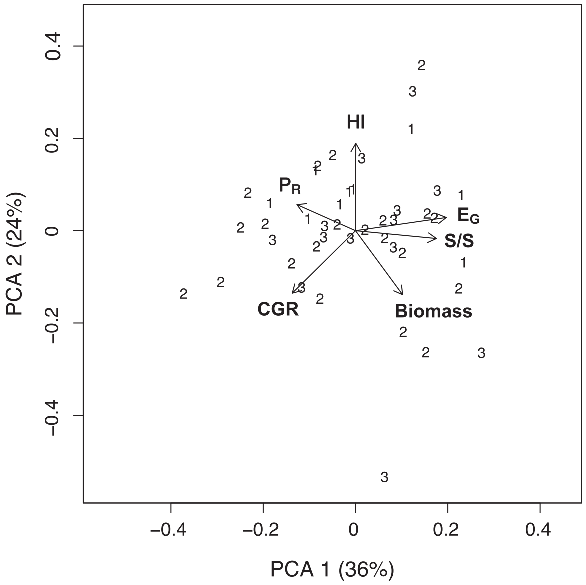

Fig. 5. Biplot of the first and second principal components based on the best linear unbiased predictor (BLUPs) for: biomass at maturity (Biomass), harvest index (HI), crop growth around anthesis (CGR), reproductive biomass partitioning (P_R), grain set efficiency (E_G) and post-anthesis source/sink ratio (S/S) for a total of 43 hybrids released from 1984 to 2014. Numbers indicate the three groups identified by hierarchical agglomerative cluster method.

Traits that were measured in only two growing conditions (biomass at maturity, harvest index, CGR, P_R, E_G and post-anthesis source-sink ratio; Table 4) were analyzed separately, and shown in Fig. 5. In general, P_R and harvest index were mutually correlated, and the same applied for CGR and biomass at maturity. P_R tented to be negative correlated with E_G. Importantly, cluster groups were dispersed across the entire biplot, showing significant variability within the groups for these other traits. Group 1 tented to be more uniform showing high values for harvest index, P_R and E_G. This was likely related to the shortest plant height and reduced time to anthesis of this group (Figs. 3 and 4). Hybrids within group 2 and 3 were very dispersed (Fig. 5). The high-yielding group (group 3) showed different strategies: high CGR and biomass at maturity, high harvest index or high E_G (Fig. 5).

4. Discussion

Genetic gain for grain yield in sorghum hybrids released in Argentina during the last 30 years was positive, averaging 8.7 kg ha^{-1} year^{-1}. A similar sorghum genetic gain has been reported in Nebraska from the period 1956–2000 (13 kg ha^{-1} year^{-1}; Mason et al., 2008). Sorghum genetic gain was similar to sunflower (12 kg ha^{-1} year^{-1}; de la Vega et al., 2007a) but lower than important crops like maize in Argentina (132 kg ha^{-1} year^{-}1; Luque et al., 2006). The genetic gain was 0.1% when expressed as percentage to the experiments mean grain yield. This value is low when compared with others crops (Duvick and Cassman, 1999; Donmez et al., 2001; Haro et al., 2013; Fischer et al., 2014), possibly reflecting differences in plant breeding research investment (Mason et al., 2008). Particularly, sorghum breeding programs in Argentina were discontinued or reduced by most seed companies in the late 1980s, but this situation changed in the late 1990s when some companies reactivated their programs (Abelardo de la Vega, personal communication). Following this, genetic yield gain seems slightly higher starting in 2000 (Fig. 1). Breeding programs were also focused on quality traits (tannin concentration, lignin content), supporting the low genetic gain.

Highest yielding hybrids, which are assumed to describe the upper boundaries of the hybrids to year of release relationships, showed no significant grain yield improvement (Fig. 1). The general low genetic gain for this species in Argentina and other countries (Mason et al., 2008; Unger and Baumhardt, 1999; Assefa and Staggenborg, 2010) highlights the importance of hybrid selection by farmers as a management practice to obtain profitable yields.

The genetic gain for grain yield was similar across environments ranging from a rainfed-low N environment (8.1 t ha^{-1}) to an irrigated-high N environment (10.8 t ha^{-1}). This is different to previous sorghum reports in the USA showing positive genetic progress for grain yield at rainfed environments (Unger and Baumhardt, 1999; Assefa and Staggenborg, 2010), but no progress under irrigated environments (Assefa and Staggenborg, 2010). We cannot conclude that the genetic progress will be the same for the diverse population of environments where sorghum is grown in Argentina, unless more experiments are repeated at lower yielding sites. Yield at rainfed-low N environment was not particularly stressful in spite of reduced N at sowing (Table 1), suggesting high mineralization rates during the crop cycle. Our results are showing that selection improved hybrid performance by minimum levels under good and intermediate growing conditions.

Global yield progress in any crop is the result of improved cultivars, crop management and on-farm adoption (Fischer et al., 2014). In Argentina, the global yield progress in grain sorghum from the same period considered in this study was 70 kg ha^{-1} year^{-1} under an average yield of 4.0 t ha^{-1} (FAO, 2014). This is high when comparing to other important producers like USA, Africa and India, in which yield progress was negligible (USA) or around 6–7 kg ha^{-1} year^{-1} (Africa and India). Although this trend, a detailed analysis focusing only in the last fifteen years also indicates no yield gains for Argentina. This is possibly associated with sorghum displacement to poorer environments and management associated with the increase in soybean area.

Differences between genetic gain and yield gain at the country level suggests that there are important non-genetic factors impacting on yield improvement, including management, climatic changes, genotype x management and genotype x environments interactions. Retrospective studies usually do not consider these interactions (Bell et al., 1995). Complementary studies taking into account these interactions and including the analyses of large historical series of trials are important. The analysis of historical data allows proper estimates of contributions of genetic and non-genetic factors (Mackay et al., 2011; Liu et al., 2013; Piepho et al., 2014).

Genetic grain yield gain was not the result of a single improved trait. Among all measured canopy traits, the genetic gain for grain yield was marginally associated with an improvement in grain set efficiency per unit of accumulated panicle biomass at anthesis, stay-green and post-anthesis source/sink ratio. These results indicate that breeding improved several grain filling attributes. The importance of breeding for post-anthesis attributes has been also evident in other species like maize (Ding et al., 2004; Luque et al., 2006) and wheat (Sadras and Lawson, 2011).

Stay-green is considered a relevant sorghum trait, and is used to select drought-tolerant materials (Rosenow et al., 1983; Borrell et al., 2000). This trait does not increase or compromise grain yield under well-watered conditions, but stay-green hybrids express higher grain yields under post-anthesis drought (Borrell et al., 2000). In the present study we found that Argentinean modern hybrids retained their leaves green longer during grain filling, which in turn resulted in a higher post-anthesis source/sink ratio. At our environments post-anthesis drought is not common, but breeding for this non-GMO species faces high insect pressure during grain filling (Maddonni, 2012) that could have contributed to this stay-green improvement. Increasing the post-anthesis source/sink ratio could have also contributed to a higher grain set efficiency through increasing grain size of late flowering spikelets (Gambín and Borrás, 2007).

In countries like Australia sorghum breeding has favored the use of short maturity stay-green hybrids to reduce lodging associated with the high frequency of terminal water stress (Henzell, 1992). Improved management practices like row configuration was also relevant for sorghum improvement (Whish et al. 2005). Our study has described an important diversity across genetic materials. By clustering groups of hybrids with similar characteristics we found three distinct groups with different strategies generating grain yield. Results are showing important opportunities for specific adaptation, although this will first require a proper environmental characterization of the target population of environments (Chapman et al., 2000; Hammer et al., 2014).

Within the group of high-yielding hybrids there are hybrids showing higher resource capture (through high crop growth around anthesis and biomass at maturity) while other showed higher resource utilization (through high harvest index, grain set efficiency or post-anthesis source/sink ratio) (Fig. 5). As recently shown for soybean cultivars (Rotundo et al., 2012), our results are suggesting there is no unique physiological pathway for achieving high yields. This gives the opportunity to compile desirable traits to develop superior genotypes toward sorghum yield improvement (Donald and Hamblin, 1976).

Finally, differences in time to anthesis across experiments were larger than expected, averaging 9 days. This could be related to hybrids differences, as hybrids were not exactly the same across environments (Table 2). Other reasons, like differences in soil moisture or soil temperature at sowing, could be also behind differences in time to emergence.

5. Conclusions

Retrospective studies are considered a powerful tool to quantify the breeding contribution to grain yield increases. They also help identify which traits have changed with selection. Significant yield variation among hybrids existed, but sorghum genetic yield progress in temperate Argentinean environments was only 8.7 kg ha^{-1} $year^{-1}$. This increase was ca. 0.1%, and can be considered low when compared with other crops. Breeding improved grain filling attributes, as modern hybrids have higher stay-green and post-anthesis source/sink ratio. They are also setting more grains per unit of reproductive biomass.

When analyzing what traits high-yielding hybrids showed irrespectively of their market release date, particular characteristics were evident: high grain number, low grain size, later flowering time, intermediate height and stay-green trait. Potential improvement could be exploited through specific adaptation and trait piramidization.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2016.01.010.

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