

# Physiological Bases of Across-Environment and Environment-Specific Responses for Grain Yield in Maize Hybrids Obtained from a Full Diallel Mating Design

Eugenia M. Munaro,\* Abelardo J. de la Vega, Karina E. D'Andrea, Carlos D. Messina, and Maria E. Otegui

## ABSTRACT

Genotype  $\times$  environment interaction explains a proportion of variation for crop yield performance often higher than the genotypic effect, becoming a major impediment to genetic progress. In this study, a crop model of yield determination in combination with three-mode principal component analysis (PCA) was used to analyze genotype  $\times$  environment  $\times$  attribute interaction. A full diallel of six maize (*Zea mays* L.) inbred lines was grown in 10 environments in Argentina. The first environment component associated with the common genotype and attribute pattern across environments revealed that the main numerical determinant of plant grain yield (PGY) was kernel weight and not kernel number per plant (KNP). The second environment component established the importance of genotype  $\times$  year interaction for anthesis-silking interval (ASI), KNP, and PGY when water deficit prevailed during the critical period of yield determination and revealed a lack of association between ASI and ear growth rate during this period. The three-mode PCA described the specific patterns of hybrid performance across environments, revealing physiological processes that separate inbred lines that contribute to drought tolerance, but at the expense of limiting PGY under well-watered conditions. The use of a crop growth model allowed interpretation of the effects of environment conditions on main physiological determinants of grain yield, exposing the effects of water supply/demand ratio as a possible driver of differential performance of inbred lines.

E.M. Munaro and C.D. Messina, Dupont Pioneer, Johnston, IA; A.J. de la Vega, Dupont Pioneer, La Rinconada, Spain; K.E. D'Andrea and M.E. Otegui, Dep. de Producción Vegetal, Facultad de Agronomía, Univ. de Buenos Aires (FAUBA), Av San Martín 4453, Buenos Aires, Argentina; K.E. D'Andrea, Consejo de Investigaciones Científicas y Tecnológicas (CONICET); M.E. Otegui, CONICET-Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Pergamino, Ruta 32 Km 45, Pergamino, Buenos Aires (2700), Argentina. Received May 14 2017. Accepted 9 Oct. 2017. \*Corresponding author (eugenia.munaro@pioneer.com).

**Abbreviations:**  $A_{\max}$ , area of the largest leaf; ASI, anthesis-silking interval; Biomass<sub>PM</sub>, biomass at physiological maturity; BLUE, best linear unbiased estimate; EGR<sub>CP</sub>, ear growth rate during critical period; G  $\times$  E, genotype  $\times$  environment interaction; G  $\times$  E  $\times$  A, genotype  $\times$  environment  $\times$  attribute interaction; G  $\times$  L, genotype  $\times$  environment interaction associated with the location effect over years; G  $\times$  Y, genotype  $\times$  environment interaction associated with the year effect; HI, harvest index; INTA, National Institute of Agricultural Technology; KNP, kernel number per plant, KW, kernel weight; PCA, principal component analysis; PGR<sub>CP</sub>, plant growth rate during critical period; PGY, plant grain yield; REML, restricted maximum likelihood;  $\sigma^2_g$ , genotypic variance;  $\sigma^2_{ge}$ , genotype  $\times$  environment interaction variance; TPE, target populations of environments; VPD, vapor pressure deficit.

**A**LTHOUGH yield progress due to plant breeding can be achieved empirically, more rapid gain could potentially be expected when some understanding of the physiological bases of crop yield performance is established and selection criteria are defined in terms of component traits (Lawn and Imrie, 1991). In heterogeneous target populations of environments (TPE), genotype  $\times$  environment (G  $\times$  E) interaction explains a proportion of variation for crop yield performance often higher than the genotypic effect, complicating selection decisions and becoming a major impediment to genetic progress. Therefore, some understanding

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of the underlying physiology of the genotype-specific responses to the environmental variation should improve the certainty of selection within a complex TPE.

The quantitative nature of grain yield and the complexity of the interactions and compensations among its main determinants pose a challenge to plant breeders when identifying indirect (trait-based) selection criteria for high yield potential and broad or specific adaptation to the program's TPE. Crop models of yield determination (i.e., based on numerical components and physiological determinants) in combination with advanced quantitative methods to analyze complex genotype  $\times$  environment  $\times$  attribute ( $G \times E \times A$ ) experiment datasets probably offer the most scope for improving the efficiency of selection in breeding programs (Wright et al., 1996).

Three-mode principal component analysis (PCA) (Tucker, 1966; Kroonenberg, 1983) has been used for interpreting genotype and  $G \times E$  interactions for multiple traits simultaneously (Kroonenberg and Basford, 1989; Basford et al., 1990; Crossa et al., 1995; Basford et al., 1996; Rincon et al., 1997; Chapman et al., 1997; de la Vega and Chapman, 2001; Cooper et al., 2001). However, as in practice, crop measurements directly related to genotype resource capture, use, or partitioning are seldom available in standard multi-environment trials; most studies applying three-mode ( $G \times E \times A$ ) PCA analysis in maize (*Zea mays* L.; Crossa et al., 1995; Chapman et al., 1997; Kroonenberg et al., 1995) were mainly focused on grain yield and secondary traits (i.e., ears per plant, ear height, plant height, and digestibility) that do not provide a functional relationship with physiological components of grain yield, with the exception of the anthesis-silking interval (ASI) (Chapman et al., 1997). Having an appropriate eco-physiological model for the ANOVA for grain yield is critical to provide insights on differences among patterns of genotypic performance and to identify specific traits or processes that are consistently associated with grain yield when evaluated in different environments.

Grain yield at maturity is related to the size of the plant (as determined by the biomass at anthesis) and the rate of biomass accumulation during grain filling, the rate of linear increase of harvest index (HI, the ratio of grain yield to shoot biomass at maturity), and the duration of the effective grain-filling period (Muchow, 1988). Furthermore, grain yield in maize is closely related to shoot biomass at harvest and kernel number per plant (KNP; Sinclair et al., 1990). Many studies have related KNP to the accumulated ear biomass 15 d after anthesis, and this accumulated ear biomass depends on the evolution of plant biomass around flowering time (Uhart and Andrade, 1995; Andrade et al., 1999; Vega et al., 2001; Borrás et al., 2007). For some genotypes, however, a weak relationship between KNP and plant growth rate during the critical period ( $PGR_{CP}$ ) for kernel set that spans between  $V_{14}$  and  $R_2$  has been reported

(Echarte and Tollenaar, 2006), indicating that kernel set was influenced by factors other than  $PGR_{CP}$  and ear growth rate during this period ( $EGR_{CP}$ ). Moreover, genotypes may present a differential response of plant grain yield (PGY) to resource availability that is not only reflected in differences in plant growth, but also in contrasting biomass partitioning to reproductive structures (i.e., HI per plant) (Maddoni and Otegui, 2006). To the best of our knowledge, studies regarding the relationship between  $PGR_{CP}$  and  $EGR_{CP}$  with HI or ASI, a reproductive trait related to HI, across different genetic backgrounds and environments are scarce. Furthermore, studies regarding the variation in mentioned relationships among hybrids of diverse genetic backgrounds are also scarce.

In this study, we used three-mode PCA in combination with physiological and numerical models of yield determination to investigate the across-environment (genotypic) and environment-specific ( $G \times E$ ) responses of a set of maize hybrids derived from Argentine flint and yellow dent inbred lines. These inbred lines were evaluated per se (i.e., not in hybrid combinations) in a previous study (D'Andrea et al., 2006), showing a strong variability in their patterns of response for morphological and physiological traits across different growing environments. The objectives were (i) to examine the across-environment pattern of associations between attributes (i.e., the physiological bases of the genotypic effect for grain yield, (ii) to describe the specific patterns of hybrid performance across environments, and (iii) to gain a partial physiological understanding of the underlying biological causes of the observed  $G \times E$  interactions by extending the analysis to a crop growth model. The goal was to identify traits whose variation regulates genotypic variation for both grain yield potential and adaptive responses to variable maize growing environments.

## MATERIALS AND METHODS

### Genetic Material, Crop Husbandry, and Experimental Design

Six maize inbred lines (B100, ZN6, LP662, LP611, LP561, and LP2) were crossed in a full diallel mating design to develop 30  $F_1$  (direct and reciprocal) hybrids. Inbred lines present per se variability for breeding era, origin, canopy size, grain yield, and grain yield components (D'Andrea et al., 2006). Lines also differ in population of origin: B100 derives from US semident germplasm (Hallauer et al., 1995), LP2 and LP561 from Caribbean  $\times$  Argentine crosses, and ZN6, LP662, and LP611 from Argentine flint germplasm. In the present study, the results will focus on hybrids only.

Field experiments were conducted at the Pergamino Experimental Station of the National Institute of Agricultural Technology (INTA), Argentina (33°56' S, 60°34' W) on a Typic Argiudoll soil, during the 2006–2007 and 2008–2009 growing seasons, and at the Manfredi Experimental Station of INTA (31°49' S, 63°46' W) on a Typic Haplustoll during

2006–2007. General environmental conditions at each site are summarized in Table 1, as well as the identification code of each treatment. Treatments were a factorial combination of 36 genotypes (30 F<sub>1</sub> hybrids and six parental inbred lines) and two N levels: control (0 kg N applied) and a high-N condition (fertilized with 200 kg N ha<sup>-1</sup>). The treatments were arranged in split-plot designs with three randomized complete blocks in Pergamino and two randomized complete blocks in Manfredi, with N availability in the main plots and genotypes in the sub-plots. Each plot consisted of three rows of 5.5-m length with an inter-row spacing of 0.7 m. Maize was hand overplanted and thinned after emergence to reach a plant population density of seven plants per square meter. Environmental variability among experiments was manipulated (crop management) by applying supplemental irrigation or dryland farming. Each combination of location × year × N × water regime was treated as a single testing site, totaling 10 environments (Table 1). The experiments were planted within the window that allows exploring environment conditions conducive to high potential yield. Maize was hand planted on 20 October and 1 November of 2006–2007 (PR02007, PR12007 and PI02007, PI12007, respectively) and 23 and 26 October of 2008–2009 (PR02009, PR12009 and PI02009, PI12009, respectively). At Manfredi, the experiments were planted on 4 Nov. 2006. Crop management did not differ between the two sites. Further details on crop husbandry for the experiments conducted in Pergamino can be found in Munaro et al. (2011).

## Measurements

Main physiological and numerical determinants of grain yield were measured. Those analyzed in this study were (i) PGY, (ii) KNP, (iii) individual kernel weight (KW), (iv) plant biomass at physiological maturity (Biomass<sub>PM</sub>), (v) HI, (vi) PGR<sub>CP</sub>, (vii) EGR<sub>CP</sub>, (viii) ASI, and (ix) area of largest leaf ( $A_{max}$ ) (Table 2). Methods for assessment of these traits are described in Munaro et al. (2011). Briefly, five successive plants were tagged at V3 on the central row of each plot, and most traits of interest were measured (e.g., Biomass<sub>PM</sub>, PGY, KNP) or estimated (e.g., PGR<sub>CP</sub> and EGR<sub>CP</sub>) from these plants. Leaf area of the largest leaf, an attribute used in modeling leaf area in crop growth models (Dwyer and Stewart, 1986; Muchow et al., 1990), was used as a proxy for leaf area per plant. Leaf area of the largest leaf was measured for length (*L*) and width (*W*) of its blade after full expansion (flowering) on tagged plants. Area was calculated using the formula  $A_{max} = 0.75LW$ . Biomass production was estimated at V<sub>14</sub> and at R<sub>2</sub> by means of allometric models (Vega et al., 2000; Maddonni and Otegui, 2004). Mean values of PGR<sub>CP</sub> and EGR<sub>CP</sub> were computed. Plants were individually harvested at physiological maturity. Plant material was oven dried at 60°C for 7 d and weighed for final shoot plant biomass determination (i.e., Biomass<sub>PM</sub>). Each grained ear was individually hand shelled, and kernel number was counted. Kernel number per plant was calculated by adding the kernels counted in apical and subapical ears (when present). Plant grain yield was computed for each harvested plant, and individual KW obtained as the quotient between PGY and KNP. For each treatment combination, we computed mean values of HI as the ratio between PGY and Biomass<sub>PM</sub>.

**Table 1. Best linear unbiased estimates of the environment mean across 15 maize hybrids obtained from a full diallel mating design evaluated in 10 environments (year × location × water regime × N combinations) in Argentina.**

Location	Environment			Trait†									
	Water	N	Year	Code	PGY	KNP	KW	Biomass <sub>PM</sub>	HI	PGR <sub>CP</sub>	EGR <sub>CP</sub>	ASI	A <sub>max</sub>
		kg ha <sup>-1</sup>			g plant <sup>-1</sup>	plant <sup>-1</sup>	mg kernel <sup>-1</sup>	g plant <sup>-1</sup>		— g plant <sup>-1</sup> d <sup>-1</sup>	—	d	cm <sup>2</sup>
Manfredi	Rainfed	0	2006–2007	MR02007	70.7	295	243	173.5	0.41	4.3	1.1	1.2	608.6
Manfredi	Rainfed	200	2006–2007	MR12007	88.3	359	259	213.9	0.41	5.2	1.2	0.8	653.7
Pergamino	Irrigated	0	2006–2007	PI02007	58.0	259	227	142.9	0.41	2.0	0.8	3.6	484.4
Pergamino	Irrigated	0	2008–2009	PI02009	105.6	420	250	274.1	0.38	4.0	2.3	4.8	712.6
Pergamino	Irrigated	200	2006–2007	PI12007	133.8	483	282	264.3	0.51	3.9	1.5	0.9	673.9
Pergamino	Irrigated	200	2008–2009	PI12009	103.8	408	254	276.0	0.37	4.1	2.3	4.9	737.9
Pergamino	Rainfed	0	2006–2007	PR02007	104.8	409	258	298.3	0.36	3.0	1.2	1.4	576.8
Pergamino	Rainfed	0	2008–2009	PR02009	35.3	233	146	151.5	0.23	3.3	1.6	6.4	634.9
Pergamino	Rainfed	200	2006–2007	PR12007	142.2	490	292	486.5	0.3	3.7	1.4	0.8	671.9
Pergamino	Rainfed	200	2008–2009	PR12009	29.5	195	146	153.3	0.19	3.2	1.3	7.5	661.3
SED‡					6.2	22	7	12.2	0.02	0.2	0.1	0.3	8.9

† PGY, plant grain yield; KNP, kernel number per plant; KW, kernel weight; Biomass<sub>PM</sub>, biomass at physiological maturity; HI, harvest index; PGR<sub>CP</sub>, plant growth rate during the critical period; EGR<sub>CP</sub>, ear growth rate during the critical period; ASI, anthesis-silking interval; A<sub>max</sub>, area of largest leaf.

‡ SED, average standard error of the difference between means.



**Table 2. Maize hybrids obtained from diallel mating design, which were evaluated in 10 environments (year × location × water regime × nitrogen combinations) in Argentina. Traits reported are best linear unbiased predictors of the hybrid means derived from a linear mixed model (Eq.[1]).**

Genotype	Trait†								
	PGY	KNP	KW	Biomass <sub>PM</sub>	HI	PGR <sub>CP</sub>	EGR <sub>CP</sub>	ASI	A <sub>max</sub>
	g plant <sup>-1</sup>	plant <sup>-1</sup>	mg kernel <sup>-1</sup>	g plant <sup>-1</sup>		— g plant <sup>-1</sup> d <sup>-1</sup> —		d	cm <sup>2</sup>
B100 × LP2	93.8	375	239	239.6	0.40	3.5	1.3	1.7	609.7
B100 × LP561	92.6	351	255	250.3	0.37	3.6	1.5	2.6	598.7
B100 × LP611	86.6	345	243	233.7	0.37	3.6	1.5	1.0	666.2
B100 × LP662	96.0	355	260	254.6	0.37	4.3	1.8	0.83	635.8
B100 × ZN6	91.5	363	244	247.3	0.38	3.8	1.5	1.3	605.8
LP2 × LP561	91.2	368	239	245.0	0.37	3.9	1.5	5.4	633.5
LP2 × LP611	79.8	334	229	237.9	0.33	3.4	1.4	5.3	677.2
LP2 × LP662	82.0	362	223	231.3	0.37	3.7	1.5	3.8	643.1
LP2 × ZN6	86.2	368	221	234.3	0.38	3.7	1.4	3.7	637.6
LP561 × LP611	82.8	333	234	244.4	0.33	3.8	1.4	5.3	659.1
LP561 × LP662	88.9	368	235	255.0	0.33	3.6	1.5	3.7	654.2
LP561 × ZN6	84.9	341	236	246.4	0.34	3.3	1.2	4.1	628.5
LP611 × LP662	72.6	335	217	219.3	0.34	3.4	1.5	3.6	659.7
LP611 × ZN6	84.7	360	223	251.6	0.34	3.4	1.3	3.2	652.9
LP662 × ZN6	93.3	369	238	260.8	0.35	3.9	1.6	3.0	662.2
SED‡	3.1	12	5	6.9	0.01	0.1	0.1	0.3	9.4

† PGY, plant grain yield; KNP, kernel number per plant; KW, kernel weight; Biomass<sub>PM</sub>, biomass at physiological maturity; HI, harvest index; PGR<sub>CP</sub>, plant growth rate during the critical period; EGR<sub>CP</sub>, ear growth rate during the critical period; ASI, anthesis-silking interval; A<sub>max</sub>, area of largest leaf.

‡ SED, average standard error of the difference between means.

## Environmental Characterization

A crop growth model as described by Cooper et al. (2016) was used to characterize the seasonal water stress patterns at Pergamino and Manfredi locations. Soil parameters that characterize water-holding capacity of the soil profile are needed as inputs to the model and were extracted from Dardanelli et al. (1997). Weather data were obtained from local weather stations at each experiment site. Only high-nitrogen treatments were simulated. A reference genotype, B100 × LP611 (Table 2), was used for model parameters related to physiological traits that affect water loss, such as canopy size and transpiration. The attribute  $A_{max}$  is used in the crop growth model to estimate leaf area per plant, which in turn is multiplied by plant density defining crop leaf area. It was assumed that the reference genotype did not present the limited transpiration trait (Gholipour et al., 2013). For those parameters related to reproductive resilience (Cooper et al., 2014), it was assumed that the reference genotype had a minimum ear biomass and maximum silk number of 1.3 g and 500 silks ear<sup>-1</sup>, respectively. The initial soil water content was calibrated using information from biomass at V<sub>14</sub> and R<sub>2</sub> stages, assuming that an increase in biomass due to grain growth is small during early reproductive stages. For each simulation, the temporal pattern of the supply/demand ratio was computed daily and used to characterize environments based on the different moisture patterns (occurrence, intensity, and duration of water deficit). Similar methodology has been used by Messina et al. (2015) to identify environment types. Daily vapor pressure deficit (VPD) was also estimated and used for environmental characterization. Silking dates were well simulated, within 1 d of observed value. The crop growth model could simulate the observed reduction in duration of the grain-filling period due to terminal drought at PR12009 (Table 1). In addition, simulated grain yield was inspected, and

the ranking of the environments based on observed grain yield matched that of simulated grain yield.

## Statistical Analysis

### Analysis of Variance

Analysis of variance was conducted to examine the partition of the phenotypic variance between genotypic and G × E interaction components for all traits, using the complete diallel mating design (i.e., 30 F<sub>1</sub> hybrids; the data obtained on the inbred lines per se were removed for the analyses reported in this study). Since exploratory analyses revealed lack of significant maternal effects in the tested germplasm (D'Andrea et al., 2009; Munaro et al., 2011), direct and reciprocal versions of each hybrid combination were pooled and considered as replicates of the same genotype. Data for all attributes were analyzed using a mixed model with environment-specific error variance (Smith et al., 2005). The phenotypic observation  $y_{ijm}$  on hybrid  $i$  in replicate  $m$  of environment  $j$  was modeled as:

$$y_{ijm} = \mu + e_j + (r/e)_{jm} + g_i + (ge)_{ij} + \varepsilon_{ijm} \quad [1]$$

where  $\mu$  is the grand mean;  $e_j$  is the fixed effect of the environment (location × year × management combinations);  $(r/e)_{jm}$  is the random effect of the replicate  $m$  nested within the environment  $j$  and is  $\sim \text{NID}(0, \sigma_{r/e}^2)$ ,  $r = 1 \dots, m$ , where  $\sigma_{r/e}^2$  is the replicate variance;  $g_i$  the random effect of hybrid  $i$  and is  $\sim \text{NID}(0, \sigma_g^2)$ ,  $g = 1, \dots, I$ , where  $\sigma_g^2$  is the genotypic variance;  $(ge)_{ij}$  is the random effect of the interaction between the hybrid  $i$  and environment  $j$  and is  $\sim \text{NID}(0, \sigma_{ge}^2)$ , where  $\sigma_{ge}^2$  is the genotype × environment interaction variance; and  $\varepsilon_{ijm}$  is the random residual effect for hybrid  $i$  in the replicate  $m$  of environment  $j$  (experimental error) and is  $\sim \text{NID}(0, \sigma_\varepsilon^2)$ , where  $\sigma_\varepsilon^2$  is the error variance. The variance components were used to evaluate the relative importance of sources of variation in the data.

Restricted maximum likelihood (REML) method (Gilmour et al., 1995) in Genstat 12.1 (VSN International, 2009) was used for estimation of the variance components of the random terms of the model and the best linear unbiased estimates (BLUEs) of the fixed environmental effects for all measured traits.

The 10 individual testing environments were analyzed separately using REML, assuming hybrids and replicates as fixed and random effects, respectively. The BLUEs of the within-environment hybrid effects for nine attributes were obtained from these analyses and further used as input data for three-mode PCA.

### Multivariate Analysis to Display the Joint Variation of Hybrids, Environments, and Attributes

Three-mode PCA (Kroonenberg, 1983) was used to evaluate the joint relative variation of hybrids, environments, and attributes using the program TUCKALS3 (Kroonenberg, 1994). A  $15 \times 10 \times 9$  three-mode, three-way  $G \times E \times A$  array of BLUEs obtained from the within-environment REML analyses was constructed using hybrids as rows, environments as columns, and attributes as slices. The efficacy of this method largely depends on the right decision about the centering and normalization of the three-way arrays. With the aim of removing the overall differences between environments and maintaining the genotypic,  $G \times E$ ,  $G \times A$ , and  $G \times E \times A$  interaction effects, the three-way array of BLUEs was centered within attributes by subtracting the across-genotype environmental means and normalized by division of the remainder by the environmental standard deviation. This process allows scaling to unit variances and eliminates the differences of scales among attributes (Cooper and DeLacy, 1994). Three-mode PCA derives components (linear combinations of the levels of the modes) for each of the three modes, which together contain the relevant systematic variation of the three-way dataset. As in this model, each mode is allowed to have a different number of components, and the number of components for each mode needs to be simultaneously determined for all modes (Kroonenberg, 1983). The adequacy of the three-mode model to fit the data, and the importance of the different components were assessed by computing the fitted sum of squares for the overall solution and for each mode separately. A parsimonious description of the dataset was sought inspecting several alternative solutions based on the increases in the fitted sum of squares compared with the increases in the number of parameters.

It is very instructive to investigate the component loadings of the genotypes jointly with the component loadings of the attributes by projecting them together in one space. The plot of the common space is called joint biplot, a variant of Gabriel's (1971) biplot for which the interpretational principals of standard biplots can be used. For the rationale behind its construction and more detailed discussion about interpretation, see Kroonenberg (1983), Basford et al. (1996), and de la Vega et al. (2002).

## RESULTS

### Environmental Characterization

Meteorological conditions differed between experimental years. Average daily maximum air temperature during the critical period of yield determination was higher in

growing season 2008–2009 (33.8°C) than in growing season 2006–2007 (29.3 and 29.5°C for Pergamino and Manfredi locations, respectively). These differences in daily maximum air temperature between growing seasons were also observed during the grain-filling period (33, 29.1, and 26.8°C at Pergamino 2008–2009, Pergamino 2006–2007, and Manfredi 2006–2007 growing seasons, respectively).

Variation between environments in evaporative demand was evident (Fig. 1). Environments from 2008–2009 growing season experienced, on average, the highest VPD during the critical period of grain yield determination (on average >2.0 kPa). Mean daily incident photosynthetically active radiation values were higher at Pergamino than Manfredi during the grain-filling period (20.1, 25.2, and 29.4 MJ m<sup>-2</sup> d<sup>-1</sup> for Manfredi and Pergamino 2006–2007, and Pergamino 2008–2009, respectively). This trend was also observed during the critical period of yield determination. Precipitation differed markedly between locations and within a same location between years, with main differences occurring during the critical period of yield determination and the grain-filling period (16.8, 41.5, and 127 mm for Pergamino 2008–2009, Manfredi and Pergamino 2006–2007, respectively, and 21.5, 132.1, and 161.2 mm for Pergamino 2008–2009 and Manfredi and Pergamino 2006–2007, respectively). The in-silico experiments allowed characterization of the environments and revealed different patterns of water stress that can occur in the Argentine Corn Belt (Fig. 2). Temporal patterns of the soil water supply to crop water demand ratio indicated severe flowering stress followed by grain-fill stress, moderate to severe grain-fill stress, and well-watered conditions at PR12009, PI12009, MR12007, and PI12007 environments, respectively. For all environments, some level of grain fill stress was present, whereas flowering stress was present only in the 2008–2009 growing season.

### Analysis of Variance

A large variation was observed across the 10 combinations of sites, years, and management practices for all measured attributes (Tables 1 and 2). Significant  $\sigma^2$  and  $\sigma^2$  were computed for all attributes (Table 3). For  $\hat{P}_{gGY}$ ,  $\hat{KNP}$ , and

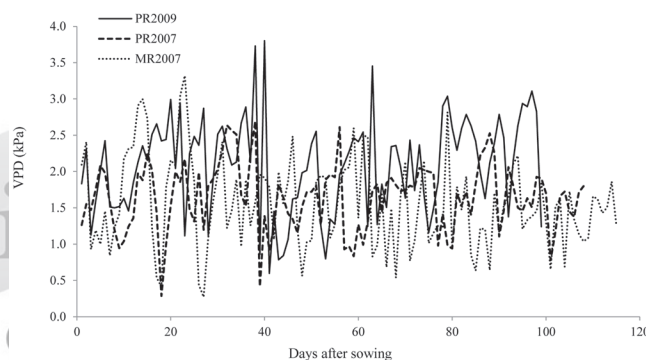


Fig. 1. Time course of vapor pressure deficit (VPD) in the three year  $\times$  location  $\times$  rainfed treatments. PR, Pergamino ; MR, Manfredi.

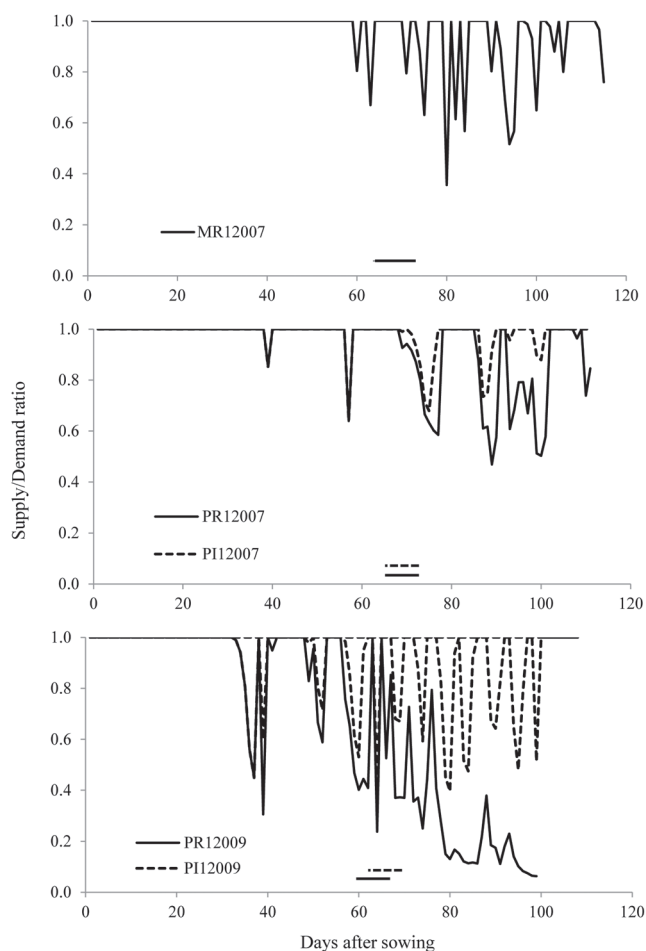


Fig. 2. Time course of supply/demand ratio for all high-N treatments at each location  $\times$  water regime combination. Soil water demand is a function of biomass accumulation, transpiration efficiency, and vapor pressure deficit. Soil water supply is a function of soil water at planting, rainfall and irrigation, and rooting depth. A supply/demand ratio of zero is complete water stress and one is no stress. Horizontal line: flowering period of the experiment. PR, Pergamino ; MR, Manfredi.

the ecophysiological traits related to kernel set ( $PGR_{CP}$  and  $EGR_{CP}$ ) and biomass partitioning (HI), the  $G \times E$  interaction component of variance was larger than the genotypic component. The genotypic effect accounted

for the highest relative portion of the treatment variation (excluding standard error) for KW,  $Biomass_{PM}$ , ASI, and  $A_{max}$  (Table 3).

### Three-Mode PCA Model Fit and Description of Components

The three-mode model with four  $\times$  four  $\times$  four components for genotypes, environments, and attributes, respectively, was considered adequate for fitting the data ( $r^2 = 0.51$ , Table 4) on the basis of informal judgements of the increases in  $r^2$  as compared with the increases in dimensions and difficulty of interpretation. When the number of components was reduced by one or more, there was a strong decrease in the multiple correlation coefficients (e.g., the three  $\times$  three  $\times$  three model accounted for only 41.9% of the variation). The variation explained by models that included four components for two of the modes was 48, 46, and 48% for the four  $\times$  three  $\times$  four, three  $\times$  four  $\times$  four, and four  $\times$  four  $\times$  three models, respectively. Increasing the environment or attribute components to five raised the  $r^2$  to only 52%. In the selected model, the four components for the genotype mode accounted for 23, 14, 8, and 6% of the variation, respectively; the four components for the environment mode for 31, 14, 4, and 3%; and the four components for the attribute mode for 29, 10, 7, and 5% (Table 4).

The components of the genotype and attribute modes (Table 4) do not have obvious interpretations, although some contrasts were evidenced. For example, the first genotypic component contrasts the hybrids of the inbred line B100 with positive scores versus those of LP611 with negative scores, whereas the second genotypic component contrasts LP611 and LP662 versus LP2 hybrids (Table 4). The first attribute component accounts for the contrast between all measured attributes versus ASI and  $A_{max}$ , and the second attribute component contrasts the main numerical and physiological determinants of grain yield (i.e., KNP and HI [positive scores] vs. KW and  $Biomass_{PM}$  [negative scores]). Treating the components of the three modes separately, however, gives only a partial view of

Table 3. Estimated variance components ( $\pm$  SE) for plant grain yield (PGY), kernel number per plant (KNP), kernel weight (KW), biomass at physiological maturity ( $Biomass_{PM}$ ), harvest index (HI), plant growth rate during critical period ( $PGR_{CP}$ ), ear growth rate ( $EGR_{CP}$ ), anthesis-silking interval (ASI), and ear leaf area ( $A_{max}$ ) estimated from 15 hybrids evaluated in 10 environments.

Attribute	Unit	Variance component†			
		$\sigma^2_g$	$\sigma^2_{ge}$	$\sigma^2_\epsilon$	$\sigma^2_{ge}/\sigma^2_g$
PGY	g plant <sup>-1</sup>	40.5 $\pm$ 19.0	43.4 $\pm$ 13.1	163.3 $\pm$ 43.5	1.07
KNP	plant <sup>-1</sup>	226 $\pm$ 147.0	567 $\pm$ 223	3099.7 $\pm$ 818.6	2.51
KW	mg kernel <sup>-1</sup>	150.4 $\pm$ 65.4	75.6 $\pm$ 29.7	520.6 $\pm$ 137.6	0.50
$Biomass_{PM}$	g plant <sup>-1</sup>	133.8 $\pm$ 64.5	79.5 $\pm$ 48.4	1429.4 $\pm$ 339.6	0.59
HI		0.0005 $\pm$ 0.0002	0.0009 $\pm$ 0.0002	0.003 $\pm$ 0.001	1.80
$PGR_{CP}$	g plant <sup>-1</sup> d <sup>-1</sup>	0.058 $\pm$ 0.032	0.175 $\pm$ 0.033	0.29 $\pm$ 0.08	3.02
$EGR_{CP}$	g plant <sup>-1</sup> d <sup>-1</sup>	0.015 $\pm$ 0.007	0.018 $\pm$ 0.005	0.11 $\pm$ 0.02	1.20
ASI	d	0.306 $\pm$ 0.126	0.204 $\pm$ 0.035	0.21 $\pm$ 0.05	0.67
$A_{max}$	cm <sup>2</sup>	571 $\pm$ 242	191 $\pm$ 92	1371 $\pm$ 361	0.33

†  $\sigma^2_g$ , genotypic variance;  $\sigma^2_{ge}$ , genotype  $\times$  environment interaction variance;  $\sigma^2_\epsilon$ , error variance.



**Table 4. Mode component scores with adequacy of fit (represented by the sum of squares, SS) for eight attributes of 15 maize hybrids grown over 10 environments in Argentina (four × four × four component model for genotypes × environments × attributes).**

Trait	Component scores			
	1	2	3	4
<b>Genotype</b>				
B100 × LP2	0.30	0.24	-0.17	-0.10
B100 × LP561	0.25	-0.05	0.11	-0.14
B100 × LP611	0.02	-0.17	-0.45	0.19
B100 × LP662	0.35	-0.56	-0.11	0.29
B100 × ZN6	0.40	0.13	-0.16	-0.03
LP2 × LP561	-0.05	-0.04	0.62	0.15
LP2 × LP611	-0.44	-0.04	0.02	-0.01
LP2 × LP662	-0.08	0.28	0.12	0.44
LP2 × ZN6	0.04	0.44	0.21	0.29
LP561 × LP611	-0.35	-0.38	0.09	-0.19
LP561 × LP662	-0.06	-0.13	0.18	-0.21
LP561 × ZN6	0.02	0.31	-0.10	-0.61
LP611 × LP662	-0.42	0.14	-0.38	0.24
LP611 × ZN6	-0.16	-0.03	-0.19	-0.09
LP662 × ZN6	0.16	-0.15	0.20	-0.13
Proportion of SS explained	0.23	0.14	0.08	0.06
<b>Environment</b>				
MR02007	0.24	-0.17	-0.72	-0.10
MR12007	0.21	-0.32	-0.31	-0.09
PI02007	0.26	-0.28	0.46	-0.60
PI12007	0.36	-0.25	0.33	0.10
PR02007	0.39	-0.28	-0.10	-0.06
PR12007	0.33	-0.25	0.14	0.74
PI02009	0.34	0.29	0.06	-0.03
PI12009	0.31	0.37	0.10	0.07
PR02009	0.40	0.30	-0.13	-0.20
PR12009	0.25	0.53	-0.04	0.05
Proportion of SS explained	0.31	0.14	0.04	0.03
<b>Attributes†</b>				
PGY	0.44	-0.12	-0.08	0.18
KNP	0.26	0.18	0.29	0.54
KW	0.37	-0.24	-0.367	-0.10
HI	0.27	0.51	0.27	0.18
Biomass <sub>PM</sub>	0.27	-0.46	-0.32	0.20
PGR <sub>CP</sub>	0.43	-0.21	0.39	-0.02
EGR <sub>CP</sub>	0.31	-0.19	0.35	-0.27
ASI	-0.40	-0.48	0.25	0.60
A <sub>max</sub>	-0.12	-0.32	0.51	-0.40
Proportion of SS explained	0.29	0.10	0.07	0.05

† PGY, plant grain yield; KNP, kernel number per plant; KW, kernel weight; HI, harvest index; Biomass<sub>PM</sub>, biomass at physiological maturity; PGR<sub>CP</sub>, plant growth rate during the critical period; EGR<sub>CP</sub>, ear growth rate during the critical period; ASI, anthesis-silking interval; A<sub>max</sub>, area of largest leaf.

the structure of the variability of the data; a simultaneous look of all modes is necessary for a full view (Kroonenberg and Basford, 1989). The joint biplots of genotypes and attributes associated with individual components of the environment mode are an efficient visual tool for the simultaneous analysis of the variation of the three modes.

The first environmental component (31% of the variation) accounts for the common pattern across environments (all positive scores); the second environmental component contrasts season 2006–2007 (negative scores) with 2008–2009 (positive scores); and the third environmental component contrasts the location Manfredi (negative scores) with Pergamino (mostly positive scores, Table 4). The fourth environmental component accounts for a fairly small proportion of the variation (3%) and does not justify discussion. Thus, the joint biplot of genotypes and attributes for the first, second, and third environmental components will be used to investigate the interactions between genotypes and attributes for all environments together (i.e., the genotypic effect), the G × E interaction associated with the year effect (G × Y), and the G × E interaction associated with the location effect over years (G × L), respectively.

### **First Environment Component: Attributes Determining Mean Plant Grain Yield across Environments**

The first and second axes of the joint biplot of genotypes and attributes for the first environmental component accounted for 18.5 and 6.3%, respectively, of the variation retained in the three-way array of BLUEs after centering and normalization (Fig. 3a). Following the convention of previous papers (Basford et al., 1990; Chapman et al., 1997; de la Vega and Chapman, 2001; Cooper et al., 2001) in this study, genotypes were represented by points and attributes by vectors from the origin.

The genotypic variability observed for PGY across environments was positively associated with the variation observed for its numerical components KW and KNP (i.e., their attribute vectors form acute angles), although the later was less retained by the system formed by the first two axes of the joint biplot (i.e., short vector; Fig. 3a). The physiological determinants Biomass<sub>PM</sub> and HI showed a positive and lack of association with PGY, respectively, and showed a negative association between them (i.e., their attribute vectors form a >90° angle; Fig. 3a). Biomass at physiological maturity and KW were positively associated in the way they discriminate among hybrids across environments, as well as KNP and HI. Both PGR<sub>CP</sub> and EGR<sub>CP</sub> showed a positive correlation to PGY; however, the shorter length of EGR<sub>CP</sub> vector indicates that this attribute was not adequately modeled by the combination of components described in joint biplot. Interestingly, EGR<sub>CP</sub> and PGR<sub>CP</sub> were associated neither with HI nor with ASI. Light-capture-related trait A<sub>max</sub> showed negative association with PGR<sub>CP</sub>, EGR<sub>CP</sub>, KNP, HI, and PGY and positive association with ASI (Fig. 3a). The angles formed by the attribute vectors ASI and A<sub>max</sub> indicated that the mean genotype values for these traits were strongly and positively correlated.

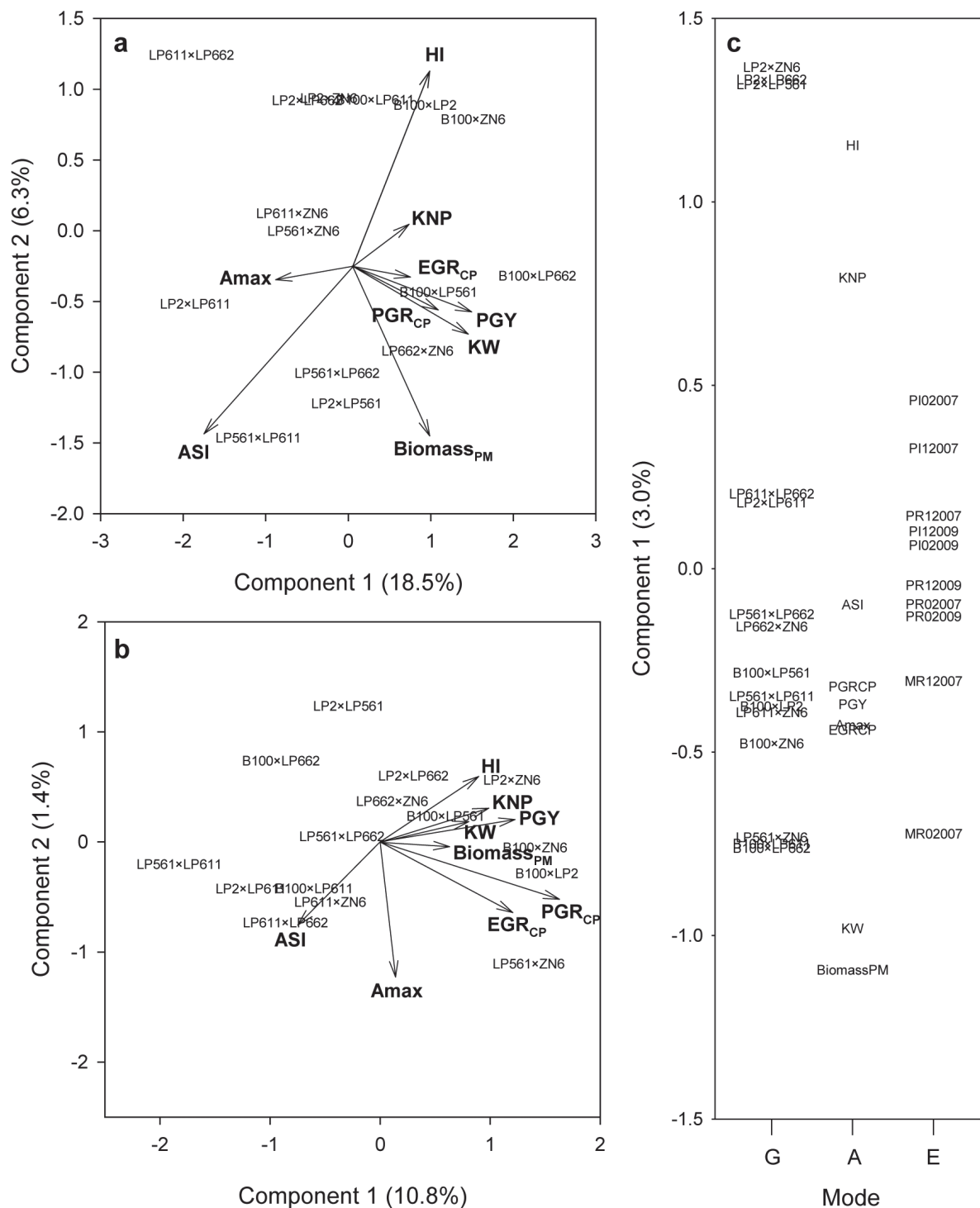


Fig. 3. Joint biplot of the (a, b) first and second or (c) first components of genotypes and attributes associated with the (a) first, (b) second, and (c) third environment components. In (a) and (b), genotypes are represented by points and attributes by vectors from the origin. See Table 1 for environment and attribute codes.

For any attribute, genotypes can be compared by projecting perpendicular from the genotype points to the attribute vector (i.e., entries that are further along in the positive direction of an attribute vector show higher values for this attribute, and vice versa). Genotypes located to the right of the diagram, in the direction of the vector of PGY (e.g., B100 × LP662), showed higher yield than those located to the left (e.g., LP611 × LP662).

To this extent, three-mode PCA allowed investigation of which inbred lines contributed the most to the observed common pattern for all locations. Hybrids developed from the yellow-dented B100 as a parental line were located on the right side of the joint biplot (Fig. 3a), showing high relative PGY and having predominantly positive projections on the HI vector, whereas hybrids that have the orange-flint LP611 as parental inbred line are located to



the left, showing low relative values for most attributes. The red-flint line LP561 is the common parent of hybrids that have a high positive projection onto the ASI and Biomass<sub>PM</sub> vectors but a low relative value for HI. Finally, the yellow semiflint LP2 hybrids intercept the HI and ASI vectors in positive and negative directions, showing high or low relative values for these traits depending on the parental line included in the cross (Fig. 3a).

### Second Environment Component: Genotype × Year Interaction

The first and second axes of the joint biplot for the second environmental component accounted for 10.8 and 1.4% of the total variation, respectively (Fig. 3b), and display those aspects of the relationships between genotypes and attributes that are influenced by the overall differences between 2006–2007 and 2008–2009 in terms of genotypic discrimination. In this joint biplot, the positive direction (indicated by arrow heads) of the attribute vectors indicates improved relative performance in 2008–2009. This is because the loadings on the second environmental component are positive for the 2008–2009 trials and negative for those of 2006–2007 (Table 4).

The second environmental component explains the most relevant pattern of G × E interaction and allows an interpretation of the changes in the relative response of genotypes in response to changes in the environment. Attributes with high loadings (positive or negative values) on the first component of the joint biplot (Fig. 3b) suggest that the genotype-specific responses for these attributes strongly determined the observed G × E interaction for yield (i.e., PGY, PGR<sub>CP</sub>, HI, and ASI were better indicators of the contrasting effects of 2006–2007 and 2008–2009 on the genotypic relative performance than A<sub>max</sub> and Biomass<sub>PM</sub>). The positive direction (indicated by arrow heads) of the ASI vector denotes a larger ASI and is negatively associated with PGY. Regarding the numerical components of yield, an improved relative performance for PGY was largely associated with higher relative values of KNP and KW. The immediate physiological determinants of grain yield, HI, and Biomass<sub>PM</sub> underlined the improved relative performance for PGY (although both HI and Biomass<sub>PM</sub> attribute vectors form acute angles with the PGY vector; the former is longer than the later, indicating better fit). An improved relative performance for PGR<sub>CP</sub> was associated with higher relative values for EGR<sub>CP</sub>. The vectors for ASI and EGR<sub>CP</sub> formed almost a right angle, indicating that these traits are orthogonal in the manner that they influence the relative responses of the hybrids to the sampled contrasting years. Genotypes located to the right of the first component axis (positive values) had a higher relative performance under the drought conditions of 2008–2009, whereas those located to the left (negative values) had a higher relative performance in the

well-watered conditions of 2006–2007. As an example, hybrids LP561 × LP611 and B100 × LP2 had high relative performance under well-watered and drought conditions, respectively. In general terms, hybrids that had B100 as a parent were located at the right side of the diagram and showed improved relative performance for PGY and all its numerical and physiological determinants in 2008–2009. LP2 hybrids, with the exception of LP2 × LP611, were positively associated with the HI and KNP vectors, indicating an improved relative performance for these traits in 2008–2009. LP611 hybrids improved their relative performance in 2006–2007 (i.e., their perpendicular projections intercept the vectors of PGY and its determinants in a negative direction).

### Third Environment Component: Genotype × Location Interaction

The first and second axes of the joint biplot for the third environmental component accounted for 3.0 and 1% of the total variation and display those aspects of the relationships between genotypes and attributes that are influenced by the differences in the way that Pergamino and Manfredi affect the relative performance of the genotypes. Since the variability explained by the second axis is too low, the major effects of the interactions captured by this environmental component can be described in a single dimension, corresponding to the first component of the joint biplot (Fig. 3c). In a case like this, the joint biplots collapse into a single line, where it is possible to include the component loadings of the environmental mode as well. In such a case, a product term to compare scores may be calculated as a product of any combination of the scores of the three modes (Basford et al., 1990; Chapman et al., 1997; de la Vega et al., 2002). For example, hybrids with positive scores such as LP2 × LP662, LP2 × LP561, and LP2 × ZN6 showed a relative increase for KW and Biomass<sub>PM</sub> (negative scores) in Manfredi testing sites (negative scores). The hybrids B100 × LP662 and B100 × LP611 (negative scores) showed a relative decrease for KW and Biomass<sub>PM</sub> (negative scores) and a relative increase for KNP and HI (positive scores) in Manfredi (negative scores). The G × L interaction effect captured by this environmental component (Fig. 3c) strongly contrasted the environment-specific genotypic responses for KW and KNP, as well as HI and Biomass<sub>PM</sub>, which was neither observed for the genotypic (Fig. 3a) nor for the G × Y interaction (Fig. 3b) effects.

## DISCUSSION

This study examined the across-environment and environment-specific responses of a set of maize hybrids to variable growing environments that comprised different years, locations, and water and N regimes. The sample of environments is a representative mixture of edaphic, climatic, and agronomic conditions that can be encountered

in the Argentine Corn Belt. The high evaporative demand resulted in the maize crop experiencing water stress even under irrigated treatments, which is often neglected in  $G \times E$  interaction studies. The reference set of hybrids obtained from the full diallel cross between lines that differ in physiological traits (D'Andrea et al., 2006) and origins revealed a wide range of contrasting genotypic responses.

### Common Genotype and Attribute Patterns across Environments

The common genotype and attribute pattern across environments (Fig. 3a) underlines the strong correlation between KW and PGY, which is not infrequent in maize (Cirilo and Andrade, 1994; Otegui et al., 1995). All environments experienced some level of water deficit during grain filling; therefore, the main numerical determinant of grain yield was KW and not KNP. This trend is in agreement with the shift from early (September–October) to late (November–December) planting registered during the last decade in the central maize production region of Argentina (PAS, 2015), which is aimed at avoiding the water deficit that usually takes place during January and affects both kernel set and the grain-filling period (Mercau and Otegui, 2014). In current research, the observed negative association between canopy size and KW may be indicating the effects of plant size on water conservation; a greater canopy size would exhaust soil water more rapidly, reducing the amount of plant-available soil water at flowering. In addition, inbred lines included in this study displayed genotypic variation for the duration of the sowing to anthesis period (D'Andrea et al., 2006), with B100 having a shorter duration (65 d) compared with the rest of the inbred lines included in the analysis (69 d). Such a strategy could have contributed to greater yield stability, as earlier-flowering genotypes could have deferred soil water use to grain filling and therefore increased KW (Borrás et al., 2004) and HI (Passioura, 1972) if water supply was limited after flowering.

### Second Environment Component: Genotype $\times$ Year Interaction

The second environment component revealed the contrast between the 2006–2007 and 2008–2009 growing seasons regarding water deficit during the critical period of yield determination. Lack of association between ASI and  $EGR_{CP}$  was observed in the determination of the  $G \times Y$  interaction, in contrast with other studies (Edmeades et al., 1993; Bolaños and Edmeades, 1996) that associated an accelerated silk emergence and a short ASI as manifestations of increased partitioning of biomass with the developing ear and of a larger ear growth rate. A plausible interpretation of the observed lack of association between ASI and  $EGR_{CP}$  is to consider the effects of water stress and high VPD on the rate of silk appearance. Anthesis–silking interval is

directly related to the process of cell expansion in the silks (Fuad-Hassan et al., 2008), and a close correlation between ASI and silk elongation rate has been reported in previous studies (Westgate and Boyer 1985, Turc et al., 2016). Furthermore, it has been suggested that whole-plant transpiration is the causal link between evaporative demand and silk elongation rate, whereas a reduction in carbon availability did not limit silk elongation rate (Turc et al., 2016). Therefore, the association between ASI and PGY could be mostly related to the effects of high VPD and/or low soil water content on the supply/demand ratio limiting silk elongation, rather than to its effect on carbon partitioning to the ear. A reduction in silk elongation could translate to asynchronous pollination (Cárcova and Otegui, 2007), leading to kernel abortion with the concomitant reduction in KNP. Differences in ASI and silk elongation rate among hybrids may determine differences in KNP independently of biomass production and partitioning. The observed correlation between  $EGR_{CP}$  and  $PGR_{CP}$  could be the result of an improved kernel set due to silk elongation rather than biomass partitioning to the ear.

Hybrids that had B100 as a parent had higher relative performance for  $PGR_{CP}$ ,  $EGR_{CP}$ , and PGY under drought conditions. The opposite holds for hybrids that have LP611 as a parent. B100 had a negative ASI, a smaller sowing-to-anthesis period, and the smallest duration of silking period as compared with the rest of the inbred lines included in this study (–0.65, 65, and 2.5 d vs., on average, 2.8, 69, and 4.6 d for ASI, sowing-to-anthesis period and duration of silking period, respectively) (D'Andrea et al., 2006). Reproductive resilience due to a small minimum ear biomass could contribute as well to the contrasting performances of hybrids (Cooper et al., 2014). In a study on silking dynamics, Rossini et al. (2005) determined that B100 had fewer ovules per ear and higher kernel number per ear than inbred line LP611 (445 vs. 600 and 287 vs. 252 for ovules per ear and kernel number per ear, respectively). Therefore, it is possible that the higher relative overall performance and higher relative performance under terminal drought of hybrids that include B100 as a parent may be related to reproductive efficiency and resilience. However, future studies should address the contribution of these attributes to the combining ability effects of PGY.

### Third Environment Component: Genotype $\times$ Location Interaction

The third environmental component allowed investigation of the contrasting effects of two types of environments, well-watered and grain-fill stress, on the main determinants of PGY. The genotypic effect (Fig. 3c) was likely associated with differences in source and sink capacity of the hybrids; therefore, KW and KNP led to rank changes of hybrids that have LP2 or B100 as parental inbred lines. B100-derived hybrids, mainly limited by canopy size (Fig.

3a), tended to have a relative lower KW and Biomass<sub>PM</sub> in environment types that had a resource limitation during grain fill, such as Manfredi (low supply/demand ratio and low incident radiation), and a relative lower KNP and HI under well-watered conditions, perhaps due to a lower potential silk number (ovules per ear), resulting in a small sink size. LP2-derived hybrids (except for B100 × LP2) were mainly sink limited in Manfredi, perhaps because of a longer duration of the silking period that may have led to asynchronous pollination resulting in kernel abortion.

## CONCLUSION

The across-environment pattern of association between attributes was examined, and KW was associated with PGY to a greater extent than KNP under water deficit induced by high VPD or low plant available soil water during grain filling. The three-mode PCA described the specific patterns of hybrid performance across environments, revealing physiological processes that separate inbred lines that contribute to drought tolerance, but at the expense of limiting PGY under well-watered conditions. The use of a crop growth model allowed interpretation of the effects of environmental conditions on main physiological determinants of grain yield, exposing the importance of VPD as a possible driver of differential performance of inbred lines.

## Conflict of Interest

The authors declare that there is no conflict of interest.

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