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PLASTICIDAD FENOTÍPICA PARA RENDIMIENTO EN GRANO Y RASGOS RELACIONADOS EN LÍNEAS E HÍBRIDOS DE MAÍZ CULTIVADOS EN REGÍMENES HÍDRICOS CONTRASTANTES

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PHENOTYPIC PLASTICITY OF GRAIN YIELD AND RELATED TRAITS IN MAIZE INBREDS AND HYBRIDS GROWN UNDER CONTRASTING WATER REGIMES

ABSTRACT

Phenotypic plasticity (PP) refers to the variation range of a trait in response to changes in the environment. Traits with low PP are classified as *stable*, whereas those with high PP are considered plastic. The objective of current research was to evaluate PP variation in grain yield (GY) and related traits among maize inbreds (I) and hybrids (H) grown under high (WW) and low (WD) water availabilities and compare it with our previous reports for N stress. Measured traits were thermal time to 50% anthesis (TT_A) and silking (TT_S), the anthesis-silking interval in days (ASI_D) and in TT (ASI_{TT}), plant height (Ph), prolificacy (Pr), GY, kernel numbers (KN), and kernel weight (KW). Data were normalized respect to the median value of each genotype group and PP computed as the difference between percentiles 90% (P_{90}) and 10% (P_{10}). As previously registered for N stress, WW data corresponded to P_{90} and WD to P_{10}, except for ASIs (opposite trend). I and H did not differ in PP only for Ph, KW and ASI_{TT}. A large plasticity (PP>1) was verified (i) for ASIs, GY and KN in response to water availability, and (ii) only for ASIs in response to N availability.

Palabras Clave
Plasticidad fenotípica, *Zea mays* L., Líneas, Híbridos.

Key Words
Phenotypic plasticity, *Zea mays* L., Inbreds, Hybrids.

INTRODUCTION

Phenotypic plasticity (PP) refers to the variation range of a trait in response to changes in the environment (Bradshaw, 1965), and it is usually expressed in relative terms respect to a reference value (e.g. the median). Traits with low PP (i.e. a narrow variation respect to the median) are classified as *stable*, whereas those with high PP are considered *plastic*. On the one hand, it can be expected the PP of a trait to be inversely related to its cost/benefit relation; i.e., that the most *plastic* traits are those that bring a large advantage at a low expense (Sadras *et al.*, 2013). On the other hand, it is generally accepted that an increase in the PP of a trait due to environmental effects (E) is linked to a reduction in its heritability (Sadras and Slafer, 2012; Sadras *et al.*, 2013), a trend usually considered unattractive by breeders. However, the main target trait of most breeding programs (GY: grain yield) is largely influenced by E, particularly through variations in resource offer (e.g. solar radiation, water, nitrogen).

PP of important cereal crops caught attention in recent years. For winter cereals plus rice, Sadras and Slafer (2012) evaluated only four GY determinants and concluded that PP declines along the cycle, from large in early-determined traits (e.g. tiller numbers) to small in the late-determined ones (e.g. individual kernel weight). In maize, D'Andrea *et al.* (2013) evaluated a large number of traits (29) for inbreds (I) and derived hybrids (H) grown under contrasting N conditions and did not verify the proposed timeline trend. Moreover, they documented that (i) I and H had a similar degree of PP for all evaluated traits, despite the usually large difference between them in the range registered for each trait, and (ii) for most traits the bottommost evaluated percentile (10%) corresponded to the poor N environment and the topmost (90%) to the rich N environment, except for developmental traits as thermal time (TT) to anthesis (TTA) and to silking (TTS) as well as the anthesis-silking interval (ASI), which had the opposite behavior.

Water availability is commonly considered the main source of variation in local maize GY (Aramburu Merlos et al., 2015). However, there is no equivalent analysis to that produced by D'Andrea *et al.* (2013) for the effects of water availability on PP of maize GY and related secondary traits. The **objective** of current research was to evaluate the variation in PP of developmental as well as growth and production traits of maize I and H grown under contrasting water regimes and compare it with our previous reports for N stress.

MATERIALS & METHODS

Field experiments were conducted at the INTA experimental station of Pocito (31.68ºS, 68.58ºW), San Juan, during 7 growing seasons (2009-2010 to 2015-2016). Evaluated germplasm across all seasons included 118 hybrid entries (78 from Dow AgroSciences and 40 from INTA, including pre-commercial cvs for the former) and 95 inbred entries (70 and 25, respectively). Sowing dates range from 1-Nov (2011-2012) to 9-Jan (2012-2013), and stand density was always 7 plants m^{-2}. Treatments were a factorial combination of (i) two genotypic (G) groups in the main plots (I and H), (ii) two water regimes (WR) in the sub-plots (WW: well-watered all the cycle; WD: water deficit from ca. anthesis – 15 days onwards), and (iii) cultivars (C) in the sub sub-plots (hereafter termed plots). Plots had 4 rows of 4 m length, with 0.7 m between rows. There were always 3 replicates. Drip irrigation was used, and WW plots received 100% of historical, daily mean potential evapotranspiration (ETo), whereas WD plots received 25% of ETo.

Measurements included: (i) dates of 50% anthesis and 50% silking on at least 10 consecutive plants of one of the central rows of each plot, used to compute cycle duration up to each event (A_{50} and S_{50}, respectively), (ii) thermal time (TT, in ºCd with a base temperature of 8 ºC) to anthesis (TT_A) and to silking (TT_S), (iii) the anthesis-silking interval (ASI), in days ($ASI_D = S_{50} - A_{50}$) and in ºCd ($ASI_{TT} = TT_S - TT_A$), both corrected to avoid negative values, (iv) plant height (Ph, in m) from the base of the stalk and including the panicle, (v) grain yield per ha (GY), based on the weight of kernels obtained from all ears present in the two central rows of each plot, standardized to 10% moisture content, (vi) prolificacy (Pr), as the number of grained ears per plant among all harvested ears, (vii) individual kernel weight (KW, in mg), based on at least 4 subsamples per plot of 100 kernels each, (vii) kernel numbers (KN) per m^2, as the quotient between GY (on a per m^2 basis) and KW.

Due to the uneven variance distribution of most traits caused by contrasting water regimes (data not shown), Kruskal Wallis non-parametric H test was used for the analysis of treatments effects. All measured traits were normalized by each corresponding median value (50th percentile) for a common comparison of PP across all evaluated environments (Sadras and Slafer, 2012). Values for percentiles 10th, 50th and 90th of each trait were identified for each genotype group (I and H). Subsequently the median value was set to 1, and the 10th (P_{10}) and 90th (P_{90}) percentiles were expressed as ratios with the median of each attribute. PP was computed as the difference between these percentiles ($PP = P_{90} - P_{10}$).

RESULTS & DISCUSSION

A significant WR effect ($P \leq 0.05$) was computed for all developmental traits. The same trend was registered for the G effect. ASI_D values of WD plots (7.9 days) more than doubled the values of WW plots (2.8 days), and I had a longer ASI (6.4 days) than H (4.30 days). TT_S and TT_A were slightly longer for I (1270 and 1357 ºCd, respectively) than for H (1229 and 1320 ºCd), and for WD (1259 ºCd and 1370 ºCd) than for WW (1240 ºCd and 1306 ºCd) plots. Consequently, ASI_{TT} differed ($P \leq 0.05$) between (i) I (81.9 ºCd) and H (91.3 ºCd), and (ii) WW (69.1 ºCd) and WD (111.4 ºCd) plots.

Strong WR and G effects were detected on growth (Ph) and production traits ($P \leq 0.0001$). The exception was Pr, for which WR caused a large difference between plots (0.92 for WW and 0.73 for WD) but no difference was observed between I (0.82) and H (0.83). As expected, H (2.06 m) were much taller than I (1.58 m), as well as WW plots (1.92 m) respect to WD plots (1.72 m). GY was markedly larger for H (5675 kg ha^{-1}) than for I (2211 kg ha^{-1}) and among WW (5734 kg ha^{-1}) than WD (2151 kg ha^{-1}) plots. Differences in GY were closely matched by trends observe in KN/m^2 (1975 for H and 571 for I; 1618 for WW and 647 for WD) and to a less extent by trends observed in KW (287 mg for H and 244 mg for I; 270 mg for WW and 252 mg for WD).

After standardization by the median, for most traits we observed that P_{90} values corresponded to WW plots and P_{10} values to WD plots, except for ASI_D and ASI_{TT} that followed the opposite trend. These results agreed with the response observed for the same traits when exposed to N stress by D'Andrea et al. (2013). Additionally, for some traits (Ph, KW, ASI_{TT}) we registered that I and H explored a similar range of variation (Figure 1), also in agreement with op.cit. for N (Figure 1 inset). There were, however, exceptions to this rule under contrasting water regimes, which corresponded to (i) TT_A, TT_S, Pr, GY and KN, due to the enhanced range (≥+17%) registered for I as compared to H (Figure 1), and (ii) ASI_D due to the enhanced range (+26%) explored by H as compared to I.

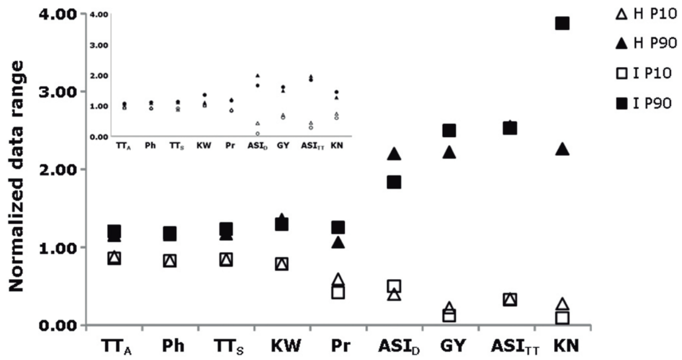

Figure 1. Normalized range of variation between the 10% (P_{10}) and 90% (P_{90}) percentiles of traits evaluated for inbreds (I) and hybrids (H). Analysis was performed across all water regimes and growing seasons. The inset corresponds to the same traits analyzed for a group of I and H developed by INTA and grown under contrasting nitrogen conditions (adapted from D'Andrea et al., 2013). Traits description in the Materials & Method section.

Described differences between I and H in the range of variation of each trait affected their PP accordingly (Table 1). Two groups of traits were defined based on the PP value, one of low (PP<1) and one of high (PP>1) plasticity. When maize crops were exposed to contrasting water regimes we observed that (i) TT_A, Ph, TT_S, KW and Pr belonged to the first group, and (ii) ASI_D, GY, ASI_{TT} and KN belonged to the second group. When exposed to contrasting nitrogen availabilities, only ASIs remained in the high PP group (Table 1).

Trait	PP_{WR}		PP_N		Mean PP
	Inbreds	Hybrids	Inbreds	Hybrids	
TT[a] to anthesis	0.35	0.28	0.132	0.114	0.22
TT to silking	0.39	0.33	0.208	0.157	0.27
Plant height	0.35	0.34	0.222	0.236	0.29
Prolificacy	0.83	0.47	0.349	0.095	0.44
Kernel weight	0.51	0.57	0.337	0.332	0.44
Grain yield[c]	**2.37**	**2.00**	0.989	0.787	**1.54**
ASI[b] in days	**1.33**	**1.80**	**1.576**	**1.558**	**1.57**
Kernel numbers	**3.78**	**1.99**	0.852	0.535	**1.79**
ASI in TT	**2.21**	**2.21**	**1.554**	**1.523**	**1.87**

[a] Thermal time; [b] Anthesis-silking interval; [c] For reference, mean values for this trait were (i) 2712 and 5715 kg ha^{-1} for inbreds and hybrids, respectively, in current research, and (ii) 3348 and 6880 kg ha^{-1} in D'Andrea et al. (2013).

Table 1. Phenotypic plasticity (PP) values computed for nine traits in hybrids (H) and inbreds (I) grown under contrasting water regimes (PP_{WR}) or nitrogen levels (PP_N) across several experimental years. PP_N values were computed from D'Andrea *et al.* (2013). Bolded values correspond to data with PP>1.

CONCLUSION

Current results confirmed the large plasticity of GY and some related traits (ASIs and KN), as well as the reduced plasticity of others (TTs, Ph, KW and Pr). Independently of the threshold used for grouping the traits (1 in current research), the proposed classification seemed valid for different growing conditions, because similar trends were detected for variable water regimes as well as soil nitrogen availabilities. ASIs values, however, were consistent among the traits with largest PP, regardless of the environmental resource responsible of GY variations.

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