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PLASTICIDAD FENOTÍPICA DE LA PRODUCCIÓN DE BIOMASA AÉREA Y SU PARTICIÓN: DIFERENCIAS ENTRE LÍNEAS E HÍBRIDOS

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PHENOTYPIC PLASTICITY OF BIOMASS PRODUCTION AND ITS PARTITIONING: DIFFERENCES BETWEEN INBREEDS AND HYBRIDS

ABSTRACT

Maize grain yield (GY) is determined by genotype (G), environment (E) and G × E interaction effects that act through the expression of three main physiological traits around flowering: plant (PGR_{CP}) and ear growth rates (EGR_{CP}), and biomass partitioning to the ears. Additionally, inbreeds (I) and hybrids (H) may differ in their responses to changes in environmental conditions. The objectives of this work are (i) to compare the phenotypic plasticity of I and H for GY, biomass production, biomass partitioning and other related ecophysiological traits, and (ii) to study the expression of absolute heterosis (H_{abs}) variations across a balanced environmental index (EI_B) built from 14 contrasting environments. A 6-inbred, complete diallel mating design was used. Phenotypic plasticity was different for I and H in all traits except harvest index and apical ear reproductive efficiency. For these traits, we detected no trend in the heterosis response to the EI_B. For traits related with biomass accumulation, H had higher mean values and plasticity than I. Instead, I showed higher mean values and plasticity for prolificacy and EGR_{CP}/PGR_{CP}.

Palabras Clave

Índice ambiental, Experimento dialélico, Maíz, Interacción genotipo por ambiente.

Key Words

Environmental index, Diallel design, Maize, Genotype per environment interaction.

INTRODUCTION

Maize GY is the product of genotype (G), environment (E) and G × E interaction effects that control the expression of its main determinants. Among the latter, maize plant grain yield (PGY) is strongly related to the number of kernels per plant (KNP) established during the critical period around flowering (Cirilo & Andrade, 1994, Otegui, 1995), This secondary trait responds to (i) plant (PGR_{CP}) and ear growth rates (EGR_{CP}) during the critical period, (ii) biomass partition to the ear (EGR_{CP}/PGR_{CP}), (iii) flowering synchrony (anthesis-silking interval, ASI) and (iv) pollination synchrony among florets within and between ears (Cárcova *et al.*, 2000). Furthermore, the response of all mentioned traits to environmental variation differ between inbreeds (I) and hybrids (H), affecting the response of heterosis across environments (Munaro *et al.*, 2011).

Environmental effects on traits can be assessed by the extent of their phenotypic plasticity. One way to evaluate phenotypic plasticity is by regressing the mean trait value of individual genotypes across a gradient of environmental indexes (EI; Finlay & Wilkinson, 1963; Eberhart & Russell, 1966). The slope (b) of the linear regression is a measure of the phenotypic plasticity. Genotypes with b=1 have an average performance and are considered stable. Those with b>1 have a greater environment response and are considered plastic, while genotypes with b<1 are those of reduced plasticity.

The objective of this work is to characterize traits related to aboveground biomass production and its partitioning in maize inbreds and related hybrids grown in complete diallel experiments, and to evaluate their performance across environments as well as environmental effects on the expression of heterosis.

MATERIALS & METHODS

Genetic material consisted in a set of (i) six inbred lines with contrasting characteristics (D'Andrea *et al.*, 2006) and (ii) the thirty derived F1 hybrids (including reciprocals). Inbreds belong to semident U.S. (B100), Argentine flint (LP611, ZN6, LP662) and Argentine flint × Caribbean (LP2, LP561) germplasm; all developed by the EEA Pergamino breeding program, except B100. The 14 explored environments were a combination of site (Manfredi, Pergamino), year (2006/07, 2008/09, 2013/14 and 2014/15), water condition (irrigated, dryland) and nitrogen level (0, 200 kg $N.ha^{-1}$). In each environment, we used a randomized complete block design with three replicates. Each plot had 3 rows of 6 m length and 0.7 m between rows. In irrigated experiments the topmost soil layer was kept near field capacity all along the cycle. In fertilized experiments, N was applied as urea at V_6. In each plot, 5 or 7 plants were tagged at V_3 for non-destructive measurements that included (i) anthesis and silking dates, and (ii) aboveground biomass per plant at ca. silking-15 days, silking, and silking+15 days by means of allometric models (Vega *et al.*, 2000). These plants were harvested at physiological maturity (PM) for assessment of (i) total biomass (BIO_{PM}), (ii) PGY, (iii) harvest index (HI= PGY/BIO_{PM}), and (iv) GY components, i.e. KNP, individual kernel weight (KW), and prolificacy (Pf, grained ears per plant). The PGR_{CP} and EGR_{CP} values were obtained from fitted allometric models.

G, E and G × E interaction effects were estimated with a multi-environmental ANOVA, fitting a mixed linear model with the package nlme version 3.1-131.1 (Pinheiro *et al.*, 2018) in R 3.4.3 (R Core Team, 2017). In each environment, I and H were compared using a *t*-test. Absolute heterosis (H_{abs}) of each trait was computed as the difference between the H trait value and the parents average trait value. A balanced environmental index (EI_B)

was computed for preventing the bias related to the uneven number of evaluated H (30) and I (6), characteristic of full-dialled designs. The EI_B values were obtained as a weighted average of I and H. The phenotypic plasticity was analysed as the linear response to EI_B of the mean trait value of each genotype group (I or H). Their responses were compared by an *F* test. Linear regression analysis was also used for evaluating the response of the Habs of each trait to EI_B.

RESULTS AND DISCUSSION

Across the 14 environments, the G × E interaction was significant for all the traits related to biomass production and its partitioning, except for Pf (table 1). Hybrids reached higher mean values than I for PGY, KNP, KW, Bio_{PM}, HI, EGR_{CP}, PGR_{CP} and KNE_1/EGR_{CP} ($p<0.05$, data not shown). Contrary, I exceeded H for the cases when significant differences were detected, in biomass partitioning to ear (i.e., EGR_{CP}/PGR_{CP}) and Pf (8 and 2 cases out of 14 environments, respectively). However, greater biomass partitioning to reproductive structures did not result in enhanced KNP of I. In most environments, I and H had similar ASI. Nevertheless, I achieved a significant lower ASI value in 3 environments. Finally, regarding the plant reproductive efficiency (i.e., KNP/PGR_{CP}), differences between genotypes were detected only in 6 out of 14 environments, with higher mean values for H in most cases.

Respect to phenotypic plasticity (i.e., I and H responses to the EI_B), there were significant differences in the *b* values of all traits ($p<0.01$), except for HI and $KNE1/EGR_{CP}$ ($p>0.05$). Hybrids plasticity exceeded I plasticity in most of the traits, except for Pf, EGR_{CP}/PGR_{CP} and KNP/PGR_{CP} (figure 1).

Trait	Genotype		Environment	G	E	G × E
	I	H		*(df = 1)*	*(df=13)*[1]	*(df=13)*[1]
PGY ($g.pl^{-1}$)	46 ± 25	93 ± 40	85 ± 42	<0.001	<0.001	<0.001
KNP ($k.pl^{-1}$)	232 ± 114	374 ± 125	351 ± 134	<0.001	<0.001	<0.001
KW ($mg.gr^{-1}$)	195 ± 42	238 ± 50	231 ± 52	<0.001	<0.001	<0.001
BIO_{PM} ($g.pl^{-1}$)	139 ± 42	220 ± 66	207 ± 69	<0.001	<0.001	<0.001
HI	0.32 ± 0.13	0.41 ± 0.12	0.39 ± 0.12	<0.001	<0.001	<0.001
Pf ($ears.pl^{-1}$)	1.09 ± 0.29	1.00 ± 0.17	1.02 ± 0.20	<0.001	<0.001	0.41
PGR_{CP} ($g.pl^{-1}.d^{-1}$)	2.34 ± 0.72	3.56 ± 1.06	3.36 ± 1.11	<0.001	<0.001	<0.001
EGR_{CP} ($g.pl^{-1}.d^{-1}$)	1.03 ± 0.46	1.35 ± 0.57	1.29 ± 0.56	<0.001	<0.001	<0.001
EGR_{CP}/PGR_{CP}	0.45 ± 0.16	0.38 ± 0.12	0.39 ± 0.13	<0.001	<0.001	<0.001
KNE_1/EGR_{CP}	235 ± 123	303 ± 118	292 ± 122	<0.001	<0.001	0.017
KNP/PGR_{CP}	105 ± 55	110 ± 39	109 ± 42	0.37	<0.001	<0.001
ASI (days)	2.9 ± 3.1	3.7 ± 3.2	3.6 ± 3.2	0.44	<0.001	0.001

I: Inbreeds, H: hybrids, PGY: plant grain yield, KNP: kernel number per plant, KW: individual kernel weight, Bio_{PM}: aboveground biomass at physiological maturity, HI: harvest index, Pf: prolificacy PGR_{CP}: plant growth rate during the critical period (CP), EGR_{CP}: apical ear growth rate during the CP, KNE_1/EGR_{CP}: apical ear kernel number per EGR_{CP}, KNP/PGR_{CP}: kernel number per plant per PGR_{CP}, ASI: anthesis-silking interval. df: degrees of freedom. [1]for ASI, 11 df.

Table 1. Mean trait values ± standard deviation and p values for fixed effects: genotype (G), environment (E) and the G × E interaction.

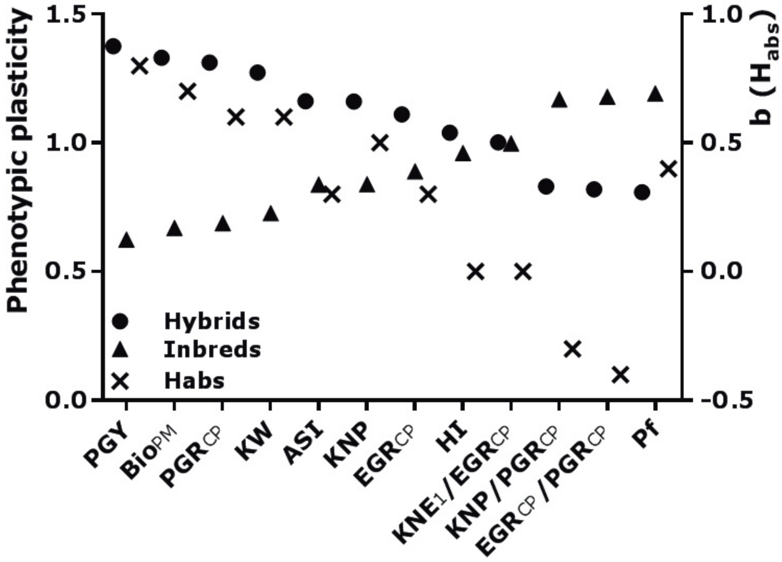

Figure 1. Phenotypic plasticity (i.e., b values of fitted linear regressions between mean trait values of each group and the balanced environmental index) and absolute heterosis (Habs) response of each trait to the balanced environmental index. Traits description as in Table 1.

The absence of differences between I and H in the response of HI and KNE_1/EGR_{CP} to EI_B was associated with the absence of a trend in the response of H_{abs} to environmental variations of the same traits, even when H have been superior to parental inbreeds. Regarding ASI, there were no differences between genotypes in high quality environments (i.e., those with reduced ASI). In restrictive conditions (i.e., low quality environments), however, ASI phenotypic plasticity of H was larger than of I. This trend was probably linked to differences in the occurrence of flowering of each group, which may have exposed hybrids to a more stressful environment than I (D'Andrea *et al.*, 2009). On the one hand, differences between I and H were emphasized in high quality environments, a response probably related to an enhanced capacity of H for taking advantage of improved growing conditions (D'Andrea *et al.*, 2009). On the other hand, I capacity to accumulate biomass was less penalized than that of H in low quality environments, probably due to their intrinsic reduced growth promoted by inbreeding depression. Finally, phenotypic plasticity in $EGR_{CP/}PGR_{CP}$ and Pf was larger for I than for H, leading to a negative H_{abs} response to the EI_B.

In conclusion, hybrid vigor determined an increase in biomass accumulation during the critical period (i. e., improved EGR_{CP} and PGR_{CP}) as well as in all traits related to final biomass (i.e. PGY, KNP, KW, BIO_{PM}), but not to an improved reproductive partitioning (i.e. EGR_{CP}/PGR_{CP}). This trend probably caused the higher Pf observed in I. However, H had a higher partitioning to reproductive structures (HI) at physiological maturity, associated with greater KNE_1/EGR_{CP} but not greater KNP/PGR_{CP}.

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