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ANÁLISIS GENÉTICO DEL PESO DE GRANO EN MAÍZ: RESPUESTA A LA DISPONIBILIDAD DE NITRÓGENO

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GENETIC ANALYSIS OF MAIZE KERNEL WEIGHT: RESPONSE TO NITROGEN AVAILABILITY

ABSTRACT

Knowing the proportion of additive effects is of interest for breeding purposes since they are the predictable portion of genetic variance. The main objective of this work was to assess the combining ability and heterosis levels for maize kernel weight (KW) and its physiological determinants under contrasting N conditions. For this purpose, 6 parental inbred lines and all possible F1 hybrids were evaluated in the field in a complete diallel mating design, at two contrasting N levels during 2013-14 and 2014-15. We found (i) significant general combining ability (GCA) effects for most traits, and specific combining ability effects for KW, grain-filling duration, maximum water content and moisture content at physiological maturity; (ii) high proportion of additive genetic variance ($\sigma_A^2 > 0.75$) for all the traits, with greater values at low than at high N level; (iii) lower additive effects as well as lower GCA-inbred performance correlation values for KW than for its physiological determinants; and (iv) a superior heterosis for KW, in addition to a greater heterosis at high than at low N level for all the traits. Selection process would be more efficient on secondary traits of KW than on KW itself, as well as under low N condition.

Palabras Clave

Zea mays L., Peso de grano, nitrógeno, Aptitud combinatoria, Heterosis.

Key Words

Zea mays L., Grain weight, Nitrogen, Combining ability, Heterosis.

INTRODUCTION

In terms of breeding, trait evaluation at the inbred level has little value if the parental inbred performance is not correlated to the hybrid progeny behavior (Hallauer and Miranda, 1988). For maize, inbred line performance is related to its behavior in hybrid combinations depending on the proportion of additive genes respect to the total variance (Falconer and Mackay, 1996). Additive effects are the predictable proportion of genetic effects, and therefore they are extensively exploited by breeders during the selection process. This process usually takes place under potential conditions. Conversely, the high environmental variability found at sub-optimal conditions (e.g. drought, low nutrient availability) affects heritability (h^2) negatively (Richards, 1996), reducing the genetic gain of the selection process (Baenziger *et al.*, 2006).

Genetic effects can be assessed by the quantification of h^2 and general combining

ability (GCA), in the case of additive effects, and of heterosis and specific combining ability (SCA) for the non-additive ones. For maize kernel weight (KW) as well as for its two main determinants (kernel growth rate –KGR– and grain-filling duration –GFD), intermediate to high h^2 values were reported (Sadras, 2007), particularly for maximum water content (MWC), KW, and KGR (Alvarez Prado *et al.*, 2013b). For these traits, genetic variability was mainly related to additive effects (Alvarez Prado *et al.*, 2013a); however, the study of the genetic architecture of KW, by means of its physiological determinants under contrasting nitrogen (N) conditions, is still lacking. The objectives of this work were (i) to quantify the combining ability and heterosis for KW and its physiological components at two contrasting N levels, and (ii) to establish the associations between GCA and inbred line performance as well as between mid-parent GCA and its hybrid progeny.

MATERIALS AND METHODS

Field experiments were conducted at INTA Pergamino Experimental Station (33°56'S, 60°34'W), during 2013-14 and 2014-2015. The experimental design was a split-plot organized in three randomized complete blocks, with N availability in the main plots, and genotypes in the subplots. Nitrogen levels were a control with no added N (N0) and a high N condition (N1), fertilized with 200 kg N ha⁻¹. The genetic mating design was a complete diallel that included six inbred lines (B100, LP2, LP561, LP611, LP662, ZN6) of different background (flint, semi-flint, dent) and all possible F1 hybrids (30). Stand density was 7 plants m⁻². A total of 12 plants were tagged in each plot, and the date of silking was registered for all these plants. The apical ears one tagged plants was collected every 5 days starting on 7 days after silking, and 15 grains per ear were sampled from the 10th (bottommost) spikelet position. Fresh and dry weights were used to calculate kernel water content and kernel moisture content, and

kernel volume (KV) was obtained by water volumetric displacement. Different models (Gambín *et al.*, 2007) were fitted to each experiment and each genotype × N × replicate: (i) a bi-linear for KW, KV, *lag* phase duration (LAG), KGR and GFD; (ii) a tri-linear for MWC; and (iii) a linear regression for kernel desiccation rate (KDR) and moisture content at physiological maturity (MCPM).

Combined analyses of variance were computed using PROC GLM in SAS. The significance of GCA, SCA and reciprocal (REC) sources of variation were determined using the corresponding interaction with the environments as error terms. The significance of GCA × environment (GCA×E), SCA×E, and REC×E interactions were determined using the residual error. Griffing's (1956) Model 1 (fixed effects) Method IV for diallel analysis was used to estimate GCA for the lines. The analysis was performed using DIALLEL-SAS05 software (Zhang *et al.*, 2005).

The proportion of additive variance (σ_A^2) on progeny performance was estimated as $\sigma_A^2 = 2\hat{\sigma}_{GCA}^2 / (2\hat{\sigma}_{GCA}^2 + \hat{\sigma}_{SCA}^2)$, where, $\hat{\sigma}_{GCA}^2$ and $\hat{\sigma}_{SCA}^2$ are the variance components for GCA and SCA, respectively (Baker, 1978). Mid-parent heterosis (MPH) was calculated as the superiority of the derived hybrid compared

to its mid-parent mean. Pearson's correlation coefficients (r) were computed to assess the relationship between inbred line and GCA. Associations between hybrid performance and GCA of inbred lines were performed by hybrid-mid-parent GCA regressions.

RESULTS AND DISCUSSION

GCA was significant for all the traits except for KV, while SCA was only significant for KW, GFD, MWC and MCPM (Table 1). By contrast, there was no effect of reciprocal crosses (REC). Environmental variations modified GCA effects, since GCA×E interac-

tions were significant for all the traits except for GFD and MCPM; anyway the magnitude of GCA effects was considerably higher than those of GCA×E interactions. SCA×E effects were significant for all the traits except GFD, LAG and MCPM.

Trait	GCA	SCA	REC	GCA × E	SCA × E	REC × E
KW	5647*	3119***	220	1469***	574***	415*
KV	5709	1710	475	2768***	802***	364**
KGR	0.016*	0.002	0.001	0.006***	0.001*	0.001
GFD	37969**	15551***	5897	5894	3221	6821***
LAG	14548**	1068	1591	2433***	1485	1504
MWC	3194*	701*	192	860***	264***	120
KDR	0.036*	0.002	0.001	0.001*	0.001*	0.001
MCPM	35.8*	12.3*	4.9	4.5	4.2	7.7**

Table 1. Mean squares of general combining ability (GCA), specific combining ability (SCA), reciprocal crosses (REC), GCA × environment (GCA×E), SCA×E and REC×E for kernel weight (KW) and its physiological components.

KV: kernel volume; KGR: kernel growth rate; GFD: grain-filling duration; LAG: lag phase duration; MWC: maximum water content; KDR: kernel desiccation rate; MCPM: moisture content at physiological maturity. ***P<0.001; **P<0.01; *P<0.05.

The σ_A^2 was high (> 0.75) for all the traits (Fig. 1A), and greater at N0 than at N1 (except for GFD). This suggests that greater selection efficiency would be expected in low N environments, as a result of an increase in the predictable portion of genetic effects. Additive variance for KW was low (0.78) in comparison with its physiological determinants, in spite of its high h^2 values reported previously (Alvarez Prado *et al.*, 2013b). Contrary, KDR and KGR values were above 0.9 at both N levels. Moreover, the greatest difference between

N0 and N1 treatments was observed for KV (0.94 vs. 0.71) and MCPM (0.88 vs. 0.72). Conversely, mid-parent heterosis (MPH) was higher at N1 than at N0, and was highest for KW (Fig. 1B). Negative MPH for KDR and MCPM was expected, since a faster KDR and a higher MCPM are related to a shorter GFD (Gambín *et al.*, 2007). However, a negative MPH for LAG was not expected, because of the positive impact of this trait on potential KW determination (Jones *et al.*, 1996).

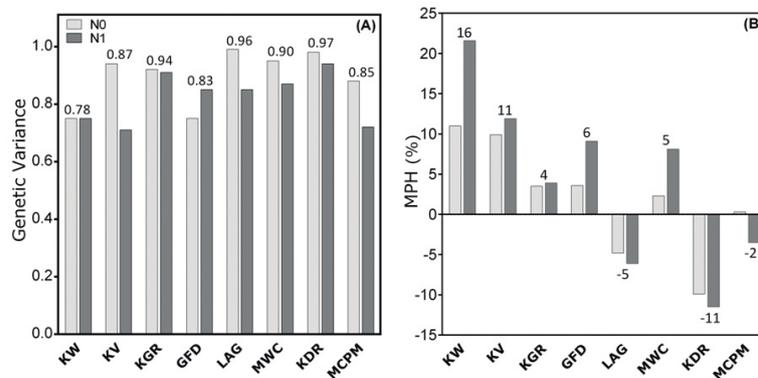


Figure 1. Proportion of additive genetic variance (A), and mid-parent heterosis (MPH) (B) for KW and its physiological determinants at high (N1) and low (N0) N levels. Value at the top of the bars represents the average across environments. Traits description as in Table 1.

The average correlations between GCA effects and inbred lines per se performance were positive for all traits (Table 2); however, there were strong differences among them ($r = 0.08 - 0.77$). For KW, the correlation was poor and lower than for its physiological determinants. On the contrary, correlation values for KGR, MWC and KDR were the

highest, and greater at N1 than at N0 level. For these traits, the high GCA–inbred line performance correlation, plus the high proportion of additive genetic control (Fig. 1A) as well as the lack of significant SCA effects (Table 1), highlight the usefulness of inbred line performance as a predictor of their hybrid progeny behavior.

N	KW	KV	KGR	GFD	LAG	MWC	KDR	MCPM
N0	0.33	0.68*	0.71*	0.29	0.05	0.70*	0.59*	0.14
N1	-0.04	0.37	0.82*	0.61	0.46	0.71*	0.67*	0.53
Average	0.08	0.46*	0.77*	0.50*	0.25	0.69*	0.63*	0.27

Table 2. Correlations between GCA and inbred performance for KW and its physiological determinants at high (N1) and low (N0) N levels, and across environments (Average). Traits description as in Table 1. * $P < 0.05$.

In agreement with previous comments for KGR, MWC and KDR, the hybrid–mid-parent GCA regressions (F1–MP_GCA) were robust for all three traits (Fig. 2). This reflects the importance of GCA effects in terms of

their magnitude, not only as a predominant component of total genetic variance, but also of the whole phenotypic expression of derived hybrids.

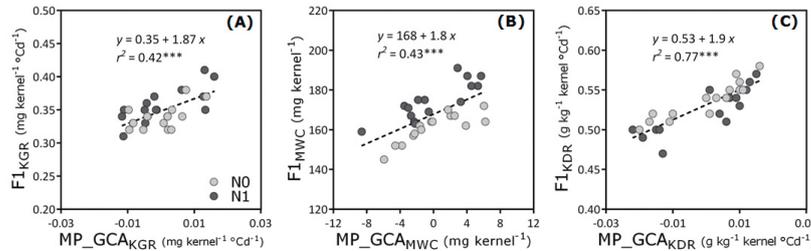


Figure 2. Relationship between hybrid performance (F1) and mid-parent general combining ability (MP_GCA) for KGR (A), MWC (B), and KDR (C) at two nitrogen levels (N0 and N1). Traits description as in Table 1. *** $P < 0.001$.

CONCLUSIONS

In this work we analyzed genetic effects underlying KW and its physiological determinants under contrasting N conditions. Unlike previous studies, we found an increase in the proportion of additive effects under sub-optimal conditions (low N availability). Likewise, this genetic effect was high for all surveyed traits, although lower for KW than for its physiological determinants. By contrast, mid-parent heterosis for KW was the highest, and increased at high N level for all the traits. The correlation between GCA and inbred line performance was lower for KW than for its determinants. This finding, in addition to the lower additive genetic control of KW, suggests that inbred line per se performance would be a better predictor of hybrid behavior for secondary traits (especially for KGR, MWC and KDR) than for KW itself.

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