PHYSIOLOGICAL DETERMINANTS OF MAIZE GRAIN YIELD: HERITABILITY AND CORRELATION ANALYSIS IN A DENT × FLINT-CARIBBEAN RILs FAMILIY

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INTRODUCTION

In maize (*Zea mays* L.), genetic improvement has been based on selection of grain yield and traits of easy measurement (e.g., plant and ear heights). This trend was accompanied by a constant increase in kernel numbers. Research on the physiological determinants of grain yield (i.e., resource capture, biomass production and biomass partitioning to grain yield; Passioura, 1996) has been usually limited to a few hybrids of narrow genetic background, and is very scarce in maize inbred lines (D' Andrea et al., 2006, 2009; Coque and Galais, 2007). The thorough understanding of the phenotypic plasticity and heritability of physiological traits related to maize grain yield is critical for assisting molecular studies aimed to improving the selection efficiency of crop breeding.

The OBJECTIVES of this research were (i) to perform a detailed phenotyping of 23 traits related to phenology, light capture, biomass production and partitioning, numerical components of plant grain yield (PGY) and N metabolism, and (ii) to establish their correlation and heritability (H^2). A family of recombinant inbred lines (RILs) of broad genetic background was used for this purpose.

MATERIALS AND METHODS

Field experiments: performed during 2009-2010 (Exp 1) and 2011-2012 (Exp 2) at INTA Pergamino research station, (33º93' S, 60º55' W), Argentina.
Treatments: a population of 191 RILs and their parental inbreds (B100: American semident; LP2: Caribbean-Argentine flint).
Experimental design: completely randomized block design with two replicates.
Crop husbandry: Stand density: 7 pl m^{-2}. Plot size between 8.4 and 10.5 m^2. Sowing dates: (i) 21-Oct-2009 in Exp 1, and (ii) 14, 18 and 23 Nov-2011 in Exp 2, for avoiding the confounded effect of inbreds variation in time to anthesis (tested in Exp 1). Sprinkler irrigation throughout the cycle. Permanent control of pests, weeds and diseases. No nitrogen (N) fertilization (soil N high in Exp 1 and low in Exp 2).
Measurements and estimated parameters: on 5 (Exp 1) or 7 (Exp 2) plants tagged at V3 in each plot, we measured traits related to:
-Phenology: Thermal time to anthesis (**TT_{ANT}**), TT to silking (**TT_{SILK}**) and anthesis-silking interval (**ASI**)
-Light capture: maximum leaf area index (**LAI_{MAX}**) and fraction of incident radiation intercepted by the canopy (**$fIPAR_{MAX}$**)
-Biomass production: plant growth rate during the critical period (**PGR_{CP}**) and total aerial biomass at V14 (**$BIOM_{V14}$**), at R2 (**$BIOM_{R2}$**) and at physiological maturity (**$BIOM_{PM}$**)
-Biomass partitioning and reproductive efficiency: ear growth rate during the CP (**EGR_{CP}**), biomass partitioning to the ear during the CP (**EGR_{CP} /PGR_{CP}**), plant biomass reproductive efficiency (**KNP/PGR_{CP}**), apical ear biomass reproductive efficiency (**KNE_1 /EGR_{CP}**) and harvest index (**HI**)
-Grain yield and its components: grained ears per plant (**prolificacy**), kernel number per plant (**KNP**), individual kernel weight (**KW**) and plant grain yield (**PGY**).
-N metabolism: total N uptake per plant at PM (**PN_{UPTAKE}**), **% protein**, **NHI**, N proportion in plant biomass (**N/$BIOM_{PM}$**), N use efficiency for grain production (**NUE**).
Statistical analyses: Mixed models analysis (SAS, 1999), Pearson's regression analysis, coefficient of variation (CV), Normality test (D'Agostino Pearson) , broad sense heritability (H^2) (Holland, 2003). Phenotypic means (BLUPs) estimated with mixed models were used for Biplot analysis using INFOSTAT program (Di Rienzo et al., 2010).

RESULTS

Significant genotypic (G), year (Y) and G×Y interactions effects (P<0.01) were detected for all measured traits, except for (i) **LAI_{MAX}**, plant biomass reproductive efficiency (**KNP/PGR_{CP}**), and biomass partitioning to the ear during the critical period (**EGR_{CP} /PGR_{CP}**) that had no significant Y effect, and (ii) **PN_{UPTAKE}** that had no G effect. There was transgressive segregation for all analyzed traits, since the RILs had values higher and lower than both parental lines (Table 1). Heritability values were (i) high (H^2>0.70) for **TT_{ANT}** and **TT_{SILK}**, **KNP/PGR_{CP}**, **EGR_{CP} /PGR_{CP}** and **KW**; (ii) intermediate (0.70>H^2>0.40) for **KNP**, **HI**, **NHI**, **PGR_{CP}**, **EGR_{CP}** and **NUE**, and (iii) low (H^2<0.40) for **PGY**, **$BIOM_{PM}$** and **PN_{UPTAKE}**. The attributes **PGR_{CP}**, **$BIOM_{R2}$**, **$BIOM_{PM}$**, **EGR_{CP}**, **HI**, **KNP** and **PN_{UPTAKE}** had a high correlation (r>0.70) with **PGY** (Table 1).

Table 1: Descriptive statistic and heritability (H^2) of grain yield and secondary traits for 191 RILs and its parental inbred lines (B100 and LP2) cropped at two contrasting environments (Exp 1 and Exp 2). r_{PGY}, phenotypic correlation with PGY. CV, coefficient of variation.

	Exp 1						Exp 2							
Trait	**B100[a]**	**LP2**	**RILs**	**Range[b]**	**CV (%)**	**N_{DP}[c]**	**B100**	**LP2**	**RILs**	**Range**	**CV (%)**	**N_{DP}**	**r_{PGY}[d]**	**H^2**
TT_{ANT} (ºCd)	954	1012	1004	891 - 1129	5.03	ns	1083	1123	1095	959 - 1228	4.56	ns	-0.57	0.81
TT_{SILK} (ºCd)	931	1066	1026	911 - 1209	5.85	ns	1052	1185	1123	1001 - 1333	5.41	ns	-0.63	0.70
ASI (d)	-1.50	3.50	1.51	-2.00 - 7.00	112	**	-2.00	3.00	1.74	-2.75 - 10.5	124	***	-0.30	0.56
LAI_{MAX}	2.79	2.61	2.69	1.54 - 4.01	18.5	ns	2.84	3.25	2.74	1.45 - 3.96	14.6	ns	0.43	0.67
$fIPAR_{MAX}$	0.73	0.63	0.66	0.35 - 0.86	14.2	**	0.77	0.65	0.74	0.50 - 0.88	8.17	***	-0.28	0.24
PGR_{CP} (g d^{-1})	3.29	2.00	2.55	1.37 - 4.35	20.6	***	2.60	2.33	2.12	1.18 - 3.35	17.3	ns	0.77	0.56
$BIOM_{V14}$ (g)	48.6	43.0	40.7	16.3 - 73.6	24.7	ns	40.4	32.0	34.9	17.4 - 59.9	23.6	**	0.58	0.23
$BIOM_{R2}$ (g)	126	108	115	65 - 182	18.4	ns	108	109	99.1	65.0 - 142	14.5	ns	0.70	0.47
$BIOM_{PM}$ (g)	150	138	150	73 - 243	18.3	ns	135	130	120	76.0 - 168	15.3	ns	0.84	0.36
EGR_{CP} (g d^{-1})	1.07	0.89	0.93	0.46 - 1.53	23.6	ns	1.08	0.83	0.81	0.30 - 1.28	24.7	ns	0.72	0.61
EGR_{CP}/PGR_{CP}	0.32	0.44	0.37	0.19 - 0.71	22.2	***	0.43	0.36	0.38	0.16 - 0.60	20.6	ns	0.20	0.76
KNP/PGR_{CP}[e]	100	170	111	20.0 - 232	31.8	***	117	160	115	19.0 - 216	33.1	ns	0.37	0.77
KNE_1/EGR_{CP}[e]	244	354	272	84.0 - 520	29.0	ns	219	440	289	54.0 - 479	31.3	ns	0.29	0.67
HI	0.42	0.43	0.36	0.07 - 0.52	23.2	***	0.35	0.40	0.33	0.07 - 0.47	26.8	***	0.77	0.57
Prolificacy	1.70	1.13	1.19	0.50 - 2.50	25.0	***	1.30	1.10	1.04	0.33 - 1.68	17.1	***	0.57	0.50
KNP	333	341	279	49.0 - 525	29.4	ns	309	350	246	39.0 - 416	31.2	*	0.82	0.60
KW (mg)	189	178	198	87.0 - 296	18.2	ns	158	157	168	71.0 - 292	20.7	ns	0.68	0.74
PGY (g)	62.3	58.4	55.5	11.4 - 96.4	26.4	ns	49.0	53.7	41.6	6.60 - 69.8	30.6	*		0.39
PN_{UPTAKE} (g)	1.59	1.51	1.60	0.59 - 3.58	22.7	***	1.23	1.00	1.03	0.68 - 1.63	16.4	ns	0.78	0.14
% Protein	10.3	9.67	10.4	7.39 - 13.2	9.58	ns	9.59	7.44	8.90	6.70 - 11.8	12.4	ns	0.58	0.62
NHI	0.64	0.62	0.57	0.20 - 0.72	18.6	***	0.58	0.67	0.56	0.12 - 0.72	22.1	***	0.69	0.56
N/$BIOM_{PM}$	10.8	10.8	10.6	8.14 - 14.1	9.78	ns	9.12	7.69	8.60	6.54 - 10.7	9.72	ns	0.55	0.47
NUE	38.7	40.2	35.4	11.4 - 52.1	23.1	**	38.6	56.1	40.5	9.00 - 60.8	27.6	**	0.40	0.52

[a] Mean values of B100, LP2 and RILs population. [b] Minimum and maximum values of RILs population. [c] D'Agostino Pearson normality test: ns, not significantly different from normal (P>0.05); *, P<0.05; **, P<0.01; ***, P<0.001. [d] all correlations significant at P<0.001 [e] KNP/PGR_{CP} and KNE_1/EGR_{CP} in kernels d g^{-1}

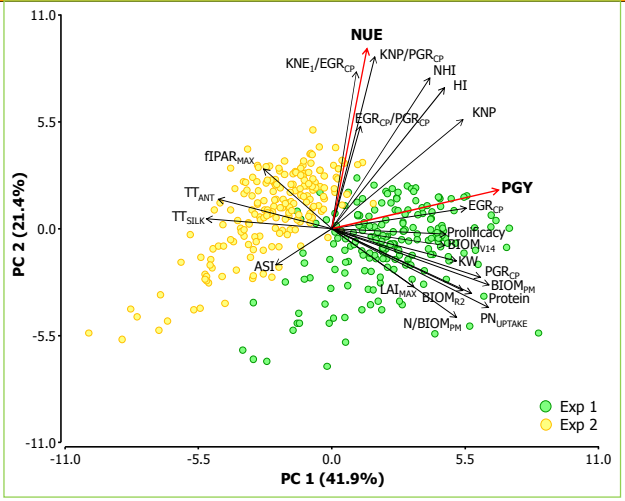

Figure 1: Biplot for the first two principal components (PC 1 and PC 2) analysis for BLUPs of 23 traits measured on 191 RILs and its parental inbred lines (B100 and LP2) cropped at two contrasting environments (Exp 1 and Exp 2). Traits are represented by vectors and genotypes by points.

The first principal component of the biplot analysis explained up to 42% of the total variance and accounted for variations in **PGY**, which were highly associated with PGR_{CP}, EGR_{CP}, $BIOM_{PM}$, KNP and PN_{UPTAKE}. The second principal component accounted for variations (21%) in **NUE**, which were highly associated with HI, NHI KNE_1/EGR_{CP} and KNP/PGR_{CP} (Figure 1).

CONCLUSIONS

In this work we phenotyped the expression of main eco-physiological and numerical determinants of grain yield in a population of RILs. We quantify the phenotypic and genotypic variability of measured attributes. Many of them (e.g., KNP, PGR_{CP}, EGR_{CP} and HI) had intermediate H^2 (0.50-0.61) and high correlation (>0.70) with grain yield. We observed that measurement of traits as PGR_{CP}, EGR_{CP} and KNP could be an advantage in less favorable environments, especially considering their early quantification as compared to grain yield. The phenotyping presented in this population is relevant for genetic studies aimed to establish associations with molecular markers used for assisting crop breeding.

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