

Untangling the Genetic Control of Maize Plant Architecture Plasticity

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Abstract

Phenotypic plasticity (PP) is the ability of an organism to produce multiple phenotypes in response to environmental changes. In cultivated species, such as maize (*Zea mays* L.), the PP of plant architecture traits will play an important role in the adaptation of genotypes to unpredictable scenarios given by climate change, marginal areas, and seeding with variable plant density (D). We bring information to improve the understanding of the environmental modulation of PPs of plant architecture traits of maize, untangling their genetic bases, and testing the hypothesis of independent genetic control of the traits per se and their PPs. The PP of traits related to leaf area, spatial distribution of leaf area and stem architecture [(leaf area (LA), maximum leaf width (LW), maximum leaf length (LL), leaf orientation value (LOV), vertical leaf angle (VA), leaf length to the flagging point (LF), LE/LL relationship (LFLL), azimuthal leaf orientation (AZ), ear height (EH), plant height (PH), EH/PH relationship (EHPH) and stem diameter (SD)] were estimated using 160 RILs from the IBM B73 × Mo17 Syn4 population, cultivated under two contrasting D (5 and 10 pl m⁻²) during two growing seasons that determined different environmental conditions. Data were phenotypically analyzed and quantitative traits loci (QTLs) were mapped. For leaf area and stem architecture related traits, high mean values of traits per se were related with high PPs values at low intraspecific competition while low mean values were observed at high intraspecific competition. The opposite response was found on leaf orientation related traits, with the exception of AZ. Forty-eight QTLs were detected for PP of plant architecture related traits on all chromosomes with exception of chromosome 7. There was no phenotypic correlation and no co-located QTLs for traits per se and their PPs. This independent genetic control for traits per se and their PPs would allow breeders to develop genotypes adapted to specific environments selecting for high or low PP in combination with high or low values for relevant agronomic traits.

1. Introduction

Maize (*Zea mays* L.) is produced worldwide in highly variable regions in terms of soils and climates, which is reflected in the average grain yield variation and in the different management practices used (Tigchelaar et al. 2018). Within the same country such as Argentina and the United States, average rainfed grain yield can fluctuate between 3.2 to 8.2 and 4.5 to 10 t ha⁻¹ considering marginal vs high potential environments, respectively (Grassini et al. 2017). In Argentina, the environments with the greatest potential for rainfed maize production involve temperate-humid climates, with a frost-free period of 240 days, average annual rainfall approximately of 950mm, a dry season concentrated in the first days of the summer and deep soils with medium textures, moderate chemical fertility and high water retention capacity (Hall et al. 1992). In these environments, the highest grain yields are reached with late winter-early spring sowing dates (early sowings) that expose the vegetative stages of maize to moderate temperatures (spring months) and the flowering stage to high daily solar radiation values (Maddonni 2012). Single cross hybrids tolerant to crowding stress and with stacked genes for protection from various biotic adversities are sown at densities (D) greater than 75000 pl ha⁻¹, and the use of fertilizers (mainly N and P) is a common a practice. Depending on predictions of spring rainfalls (e.g., “Niña” phase of the ENSO phenomenon), the characteristics of the land used (e.g., low soil water content at the end of winter fallow), or business decisions (e.g., diversification of risks), sowing date may be delayed to late-spring or early summer (late sowings). At late sowings, maize vegetative growth is exposed to high temperatures of early summer season and flowering to moderate daily solar radiation values of late summer days (Maddonni 2012; Otegui et al. 2021), and farmers commonly cultivate the same hybrids sown at early sowings at a similar or slightly lower D.

In contrast, marginal environments encompass regions that are more restrictive in terms of water supply, due to a lower quantity (less than 700 mm year⁻¹) and erratic distribution of rainfall and/or soils with lower water storage capacity and fertility. In these environments, the most frequent technological package is the late sowing of maize crops at low D (< 55000 pl ha⁻¹), uncommon use of fertilizers, and in many cases, using the same hybrids that in early sowing dates. Therefore, the same maize hybrids can be used in contrasting environments, adjusting sowing date, D and nutrient

supply, all factors that modify the vegetative and reproductive growth of maize plants (Uhart and Andrade 1995; Maddonni and Otegui 1996; Maddonni et al. 2001b; Parco et al. 2020; Rotili et al. 2021). For example, the maize plant phenotype at low D, presents a stem with short and wide internodes, short and wide leaf blades with a planophile leaf angle, random azimuthal leaf orientation, and one or two fertile ears per plant (according to the prolificacy of the genotype). In contrast, the maize plant phenotype at high D, given the higher competition for resources among neighboring plants, is characterized by a stem with long and thin internodes, long and narrow erectophile leaves oriented azimuthally toward the interrow, and a single fertile ear per plant (Tetio-Kagho and Gardner 1988a; Tetio-Kagho and Gardner 1988b; Andrade et al. 1999; Maddonni et al. 2001a2007; Ciancio et al. 2016). This reactivity of maize architecture traits to the presence of neighbors maximizes the capture of resources per plant (e.g., water, radiation and nutrients) at low D (Andrade and Ferreiro 1996; Rotili et al. 20192020; Wies and Maddonni 2020). At high D, competition among plants is intensified (Pagano et al. 2007), but crop resource capture is maximized (Andrade et al. 1999; Maddonni and Otegui 2006; Maltese et al. 2020; Parco et al. 2020). At low D, plants exhibit a high growth rate around flowering, which determines a high kernel number per plant (Andrade et al. 1999; Ciancio et al. 2016). By contrast, at high D despite the low growth rates of plants, crop growth rate around flowering and consequently kernel number per unit area and grain yield are maximized (Andrade et al. 1999; Maddonni and Otegui 2006). However, at higher D, penalties on kernel number per unit area, promoted by barren plants (Vega and Sadras 2003), could be avoided or higher kernel number per plant could be obtained by selecting genotypes with a compact plant architecture, improving light penetration at ear leaf strata (Cagnola et al. 2021) and reducing stalk lodging (Xue et al. 2021). Taller plants with thinner stems and high ear height (EH), typical of high D, can increase the risk of stalk lodging, that produces annual grain yield losses of approximately 5–20% globally (Flint-Garcia et al. 2003). Hence the best ideotype to fit crop grain yield across environments would exhibit high reactivity of some plant architecture traits (avoiding an exacerbated plant elongation), i.e. phenotypic plasticity (PP) (DeWitt and Scheiner 1998).

According to Monforte (2020), the degree of PP can vary from zero (the phenotype is stable) to far from zero (the phenotype is plastic) and such variation in PP is classically known as genotype \times environment interaction. Low PP in grain yield (i.e., grain yield stability across environments) could be related to high PP in other traits involved in the capture and use of resources, such as root size and root distribution (Shao et al. 2019; Pires et al. 2020), plant height and leaf size, leaf anatomy, and leaf physiology (Pires et al. 2020). However, if PP of these traits have a penalty on grain yield, PP would be undesirable to be selected (DeWitt et al. 1998). Particularly for maize crops at high D, Wies and Maddonni (2020) evaluated if PPs of plant architecture traits generated for shade avoidance responses triggered at HD (i.e., thinner stems, plant elongation, leaf area, leaf anatomy), are detrimental or beneficial for plants growth and plant grain yield. They found that shade avoidance responses do not have any detrimental effect on grain yield because plant growth rate around flowering and kernel number per plant were sustained by the different ability of plants to capture light (i.e., high PPs of plant architecture traits).

Genetic basis for maize plant architecture traits (all quantitative traits) were studied in several works and reviewed in a recent paper (Incognito et al. 2020). PP is also a quantitative trait (Kliebenstein et al. 2002; Ordas et al. 2008; Rönnegård and Valdar 2012 ; Shen et al. 2012) with a genetic control partially independent of the trait per se (Bradshaw 1965). This fact was documented for several species and traits, such as transpiration in grapevine (Marguerit et al. 2012), flowering time and fruit weight in tomato (Diouf et al. 2020), and leaf expansion (Reymond et al. 2003), kernel growth (Alvarez Prado et al. 2014) and grain yield in maize (Kusmec et al. 2017). Important consequences derive from the partial independence of the genetic control of the trait per se and PPs, since PP can evolve independently of the changes of the trait per se and breeders could select a genotype combining a certain target trait with high or low PP. Additionally, to our knowledge there is few information on the relationship between maize plant architecture traits per se and their PPs at different environmental conditions. The objectives of this work were to (i) study PP of maize plant architecture traits using the IBM (B73 \times Mo17) Syn4 recombinant inbred lines (RILs) public population, ii) investigate the relationship

between traits per se and their PPs, as well as the environmental modulation of this relationship, and iii) compare the genetic control of the traits per se (Incognito et al. 2020) and their PPs.

2. Materials And Methods

2.1. Experimental design and growing conditions

We used a multi-trait phenotypic data set composed by 160 RILs from the IBM (B73 × Mo17) Syn4 maize population grown at two densities (5 and 10 pl m⁻², low D and high D; respectively) during two growing seasons, 2013/2014 and 2014/2015, at the experimental fields of the Universidad Nacional de Lomas de Zamora (34° 49 S, 58 ° 43 W, Typical Argiudol) and the Department of Crop Production of the Universidad de Buenos Aires (34° 35 S, 58° 29 O, Vertic Argiudol), Buenos Aires, Argentina.

A split plot design was used with D assigned to the main plots and genotypes to the sub-plots, arranged as randomized complete blocks with three replications. The experiments were manually sown on 1 December 2013 and 30 December 2014. Two seeds were sown per position and then thinned to one plant at the three-ligulated leaf stage (V3; Ritchie et al. 1993). Each sub-plot included 3 m long rows 0.5 m apart. Crops were irrigated along the cycle and nitrogen fertilization (200 kg N ha⁻¹) was applied at V4 to minimize N restrictions. Weeds, diseases and insects were chemically controlled. Thus, Ds and seasons were combined to generate different growing conditions for vegetative plant growth. Measurements of meteorological conditions were registered using data from meteorological station located in Ezeiza (Buenos Aires Province) and Buenos Aires City for the first and second growing seasons, respectively. As was described in Incognito et al. (2020), mean incident solar radiation (5.5%) and air temperature (2%) were slightly higher during the first growing season, but largest differences between seasons were recorded during the vegetative growth period (higher during the first than during the second season).

2.2. Measurements of architecture plant traits

Immediately after female flowering (Beavis et al. 1991; Ritchie et al. 1993), four plants of the middle row of each sub-plot were selected to quantify architecture plant traits. Measurements of leaf architecture were recorded at the ear leaf strata, involving the leaf subtending the apical ear, plus two leaves above and below. Traits involved maximum leaf width (LW), maximum leaf length (LL), azimuthal leaf orientation (AZ), vertical leaf angle at stalk from the horizontal plane (VA) and leaf length to the flagging point (LF). For AZ, a 180° protractor was used, positioning the 0°–180° line on the row direction and the center of the protractor on the stem of each plant below each leaf to be measured. The AZ was registered from the angle formed by the orientation of the middle part of the central rib of the leaf. In this way, AZ values close to 90° indicate leaves perpendicular to the row and those close to 0° or 180° indicate leaves parallel to the row (Girardin and Tollenaar 1994). LW and LL were used to estimate leaf area (LA) based on method proposed by Montgomery (1911); LW, LL, VA and LF were used to estimate leaf orientation value (LOV) as in Pepper et al. (1977) and the ratio between LF and LL (LFLL) was also computed. Stem architecture traits involved ear height (EH) and plant height (PH) from soil level, and stem diameter (SD) at the base of the plants. The ratio between EH and PH (EHPH) was also computed. For each trait, phenotypic values of each RIL were reported as the average of four plants per sub-plot.

2.3. Quantification of phenotypic plasticity of architecture plant traits

For each RIL, PP of each trait was estimated using the coefficient of relative plasticity proposed by Réale and Dingemans (2010) (Eq. 1).

$$\text{coefficient of relative plasticity} = \frac{V_{\text{RIL}}}{V_{\text{P}}} \text{ Eq. 1}$$

where V_{RIL} is the variance of each RIL for the evaluated trait and V_{P} is the overall phenotypic variance of the RILs population.

Hence, the coefficient of relative plasticity of each trait (hereinafter referred to as the abbreviation of a trait followed by P as subscript, for example LA_{P}), returned 160 values of PP. The coefficient of relative plasticity values are similar measures to reaction norms which do not require assumptions on their shape (Sadras and Lawson 2011; Sadras and Rebetzke 2013; Sadras and Richards 2014).

Relationships between population variability of traits and their PPs, estimation of descriptive statistics of PP, and correlations between traits or PPs were performed using R software version 4.1.0 for Windows (R Core Team 2021). Linear and bilinear regressions were fitted to the relationship between median PP vs statistics descriptors and heritability of traits per se (see 2.4) vs median PP, using GraphPad Prism 6.00 program for Windows. Additionally, to study the relationship between maize plant architecture traits per se and their PPs at different environmental conditions, linear regressions were fitted to the 10th and 90th percentiles of each trait per se and the corresponding median PP (Sadras and Richards 2014). For each PP of each RIL, trait data set comprised 12 data (two D, three blocks, two seasons).

2.4. Heritability of plant architecture traits and their phenotypic plasticity

The broad-sense heritability (Eq. 2) of each trait was estimated using a mixed model that considered genotypes, environments (D × season combination) and blocks nested within environments, and genotype × environments interaction as random effects.

$$H^2 = \frac{\sigma_{\text{G}}^2}{\left(\sigma_{\text{G}}^2 + \frac{\sigma_{\text{GE}}^2}{n} + \frac{\sigma_{\text{E}}^2}{bn} \right)} \text{ Eq. 2}$$

where σ_{G}^2 is the genotypic variance, σ_{GE}^2 is the genotype × environment variance, σ_{E}^2 is the residual variance and n and b are the number of environments and the number of blocks, respectively (Hallauer and Miranda Filho 1988).

The variance of PP is composed by the environment and genotype × environment variances. Thus, considering that genotype × environment variance constitutes the heritable component of PP variance (Scheiner and Goodnight 1984), heritability for PP of each trait was estimated by Eq. 3.

$$H^2 = \frac{\sigma_{\text{GE}}^2}{\sigma_{\text{P}}^2} \text{ Eq. 3}$$

where σ_{GE}^2 is the genotype × environment variance and σ_{P}^2 is the phenotypic variance.

2.5. Genetic analysis of phenotypic plasticity of plant architecture traits

Quantitative trait loci (QTLs) analysis was used to determine the genomic regions associated to PP, using the genetic map generated by Incognito et al. (2020) which considered 1158 markers distributed equally along the entire genome

according to the Maize GDB website (<http://www.maizegdb.org>). The QTL mapping was carried out for each PP using multi-trait composite interval mapping (MT-CIM) procedure of WinQTLCartographer V2.5 (Wang et al. 2012) choosing model 6 of the Zmapqtl procedure. The genome was scanned every 1 cM using a 10 cM window and a LOD = 2 to declare the presence of a significant QTL. This threshold was used because PP of each trait show low heritability estimates with a consequently low power to detect QTLs (Beavis 1994). The phenotypic variation and additive effect explained by each QTL were estimated at the value corresponding to the QTL peaks obtained from MT-CIM. The QTL found for PP of each trait was compared with the QTLs for the traits per se reported by Incognito et al. (2020). To investigate the genetic overlap (co-location) between QTLs of traits per se with QTLs of PP of each trait, we compared 1 LOD support intervals for detected QTLs (Li et al. 2016; Raihan et al. 2016) and so, a colocation was declared if the intervals of two QTLs overlap. Final position of QTL was declared as the average of the most probable location of the QTLs peaks between co-located QTLs.

3. Results

3.1 Phenotypic plasticity of plant architecture traits and correlation between heritability of traits per se and the median phenotypic plasticity values

A great variation of PP was found among evaluated traits and within each trait (Fig. 1). The AZ_p and SD_p showed the higher values and VA_p and LOV_p the lower values with a positive and a negative biased of ca. 30, 26, and 38% from mean PP (0.77), respectively (Fig. 1 and Table 1). PP distributions with high positive skewness and high kurtosis values corresponded mainly to traits with lower PP values, such as LOV and VA. Thus, the highest CV, skewness and kurtosis values of PP were recorded for traits with the lower median PP values (Fig. 2 and Table 1).

Table 1

Descriptive statistics for phenotypic plasticity of leaf area (LA_p), leaf width (LW_p), leaf length (LL_p), leaf orientation value (LOV_p), vertical angle (VA_p), relationship between leaf to flagging point (LF_p) and LL ($LFLL_p$), LF_p , azimuthal orientation (AZ_p), relationship between ear height (EH_p) and plant height ($EHPH_p$), EH_p , PH_p , and stem diameter (SD_p) 160 RILs from IBM B73 × Mo17 Syn4 population

Trait Plasticity	Mean	Median	Minimum	Maximum	Range	CV	Skew	Kurtosis
LA_p	0.83	0.8	0.19	2.54	2.35	47.5	1.11	1.92
LW_p	0.73	0.68	0.14	2.36	2.22	49.2	1.06	1.87
LL_p	0.78	0.69	0.14	2.56	2.42	55.8	1.51	2.71
LOV_p	0.55	0.46	0.05	2.5	2.45	67.6	2.12	7.27
VA_p	0.48	0.38	0.07	3.16	3.09	83.9	2.99	13.97
$LFLL_p$	0.71	0.62	0.07	2.44	2.37	61.5	1.35	1.96
LF_p	0.83	0.75	0.18	3.31	3.13	51.7	1.73	6.1
AZ_p	1	0.96	0.18	2.33	2.15	40.0	0.51	0.03
$EHPH_p$	0.78	0.69	0.17	2.48	2.31	52.7	1.28	1.87
EH_p	0.82	0.75	0.15	2.15	2	44.4	1.04	1.35
PH_p	0.8	0.76	0.23	2.03	1.8	43.7	1.04	1.4
SD_p	0.97	0.89	0.23	2.37	2.14	43.4	1.21	1.41

A negative relationship between heritability of traits per se and the median PP values was observed (Fig. 3a). Linear and bilinear models were fitted to this relationship, but better described by the bi-linear model yielding a first slope value not different from zero (i.e. heritability of trait per se was not associated with median PP) but a second negative slope value significantly different from zero for traits with median PP values higher than 0.84 (i.e. heritability of trait per se was lower for those traits with high median PP, such as AZ and SD) (Fig. 3b).

3.2. Correlations among plant architecture traits per se and their PPs

Correlations among plant architecture traits are graphically described in Fig. 4. Mean values were previously documented in Incognito et al. (2020). Briefly, variability of LA was more related (positively) to LL ($r = 0.87$) than to LW ($r = 0.61$); LOV was more related (positively) to VA ($r = 0.89$) than to LFLL ($r = 0.69$); PH was positively related to EH ($r = 0.85$) and weakly related to SD ($r = 0.21$) and AZ was not related to the other plant traits.

Relationship between traits per se and PPs resulted positive and significant for LA, EH and SD and negative and significant for VA, LF and LFLL (Table 2).

Table 2

Pearson correlation coefficient (*r*) and significance (*P*-value) for the relationship between traits per se and phenotypic plasticity for leaf area (LA), leaf width (LW), leaf length (LL), leaf orientation value (LOV), vertical angle (VA), relationship between leaf length to flagging point (LF) and LL (LFLL), LF, azimuthal orientation (AZ), relationship between ear height (EH) and plant height (PH) (EHPH), EH, PH and stem diameter (SD)

Trait	Phenotypic plasticity	
	<i>r</i>	<i>P</i>
LA	0.22	**
LW	0.08	ns
LL	0.03	ns
LOV	-0.07	ns
VA	-0.18	*
LFLL	-0.44	***
LF	-0.17	*
AZ	0.1	ns
EHPH	-0.09	ns
EH	0.36	***
PH	0.13	ns
SD	0.26	**

The significance levels are indicated by symbols: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, ns: no significant.

3.3. Environmental modulation of the relationships between plant architecture traits per se and their PP

Linear regressions were fitted to the 10th and 90th percentile data set of each trait and RIL and its PPs. The slope values were used to describe the capacity of each trait to capture favorable and unfavorable environmental conditions (Figs. 5–7). The contrasting environments were established based on the expected response of each trait to environments of high intraspecific competition and low intraspecific competition, and consequently the 10th or 90th percentile dataset of each trait was classified as representative of these environments (Table 3). A similar absolute slope value for 10th and 90th percentiles, would reflect a symmetrical reaction of the trait to unfavorable and favorable conditions. For example, LA slope values varied from -40 cm^2 to 69 cm^2 for the 10th and 90th percentile, respectively (Fig. 5a). Thus, for this combination of RILs and environments, LA showed an asymmetrical reaction to favorable (higher response) and unfavorable (lower response) environmental conditions. By contrast, for LW and LL, similar slope values for 10th and 90th percentiles suggest a symmetrical capacity to capture contrasting environmental conditions (Fig. 5b, c).

Table 3
Expected environmental conditions represented by the 10th (P10) and 90th(P90) percentiles

Trait Group	Traits	P10	P90
Leaf area	LA	High intra-specific competition	Low intra-specific competition
	LW	High intra-specific competition	Low intra-specific competition
	LL	High intra-specific competition	Low intra-specific competition
Spatial distribution	LOV	Low intra-specific competition	High intra-specific competition
	VA	Low intra-specific competition	High intra-specific competition
	LFL	Low intra-specific competition	High intra-specific competition
	LF	Low intra-specific competition	High intra-specific competition
	AZ	High intra-specific competition	Low intra-specific competition
Stem architecture	EHPH	High intra-specific competition	Low intra-specific competition
	EH	High intra-specific competition	Low intra-specific competition
	PH	High intra-specific competition	Low intra-specific competition
	SD	High intra-specific competition	Low intra-specific competition

High responses to favorable environmental conditions were obtained for LOV and associated traits, but moderate or null responses were found to unfavorable conditions (Fig. 6a-d). In contrast, AZ showed an almost symmetrical response to capture favorable and unfavorable environmental conditions (Fig. 6e).

All stem architecture related traits showed an asymmetrical response to environmental conditions, high (or low for EHPH) response for favorable environments but moderate (or higher for EHPH) or null to unfavorable environmental conditions (Fig. 7).

3.4. QTL mapping for phenotypic plasticity of plant architecture traits

Heritability for PP of plant architecture traits showed low to mid values. For LA_p related traits, heritability values were 0.4 for LA_p, 0.25 for LW_p, and 0.5 for LL_p. For LOV_p related traits, heritability values were 0.18 for LOV_p, 0.20 for VA_p, 0.34 for LFL_p and 0.4 for LF_p. For AZ_p, heritability value was 0.29. The PP of stem architecture related traits showed heritability values of 0.31 for EHPH_p, 0.21 for EH_p, 0.21 for PH_p, and 0.59 for SD_p.

Forty-eight QTLs were detected for PP of plant architecture traits on all chromosomes with exception of chromosome 7 (Fig. 8 and Table 4). From 1 to 7 QTLs were detected for each PP traits, accounting from 5.6 to 15.7% of PP variation. No epistatic interactions were detected among these QTLs.

Table 4

Summary of detected plasticity quantitative trait loci (PQTLs) for plasticity of leaf area (LA_p), maximum leaf length (LL_p), vertical angle (VA_p), relationship between leaf to flagging point (LF_p) and LL ($LFLL_p$), LF, azimuthal orientation (AZ_p), relationship between plant height (PH_p) and ear height (EH_p) $EHPH_p$, EH_p , PH_p , and stem diameter (SD_p) for 160 RILs from IBM B73 × Mo17 Syn4 population.

Trait	Chromosome	Position (cM)	One LOD interval (cM)	Co-located PQTLs ^a	Co-location between PQTLs and MT-QTLs detected in Incognito et al. (2020) ^b	Nearest marker	LOD	PVE (%) ^c	Additive effect ^d
LA_p	3	0.42	0.40–0.48	a		bnl8.15	2.67	7.4	0.10
	4	0.58	0.57–0.61			AY109715	2.18	6.1	-0.09
	5	2.27	2.18–2.28	b		ufg99F-220-C12	3.69	10.1	-0.11
	8	1.16	1.14–1.21	c		csu332	2.46	6.8	0.10
	10	0.97	0.94–0.98	e		mmpP4B06	2.36	6.6	0.09
LL_p	2	2.52	2.51–2.53			UMC2246	2.50	7.0	0.10
	3	0.45	0.43–0.78	a		bnl8.15	3.22	8.9	0.12
	5	2.26	2.16–2.28	b		ufg99F-220-C12	3.48	9.5	-0.13
	8	1.01	0.96–1.03			csu332	2.57	7.1	0.13
	8	1.06	1.05–1.08			csu332	3.91	10.6	0.13
	8	1.16	1.16–1.22	c		csu332	2.86	7.9	0.11
	10	0.97	0.96–0.98	e		mmpP4B06	2.27	6.3	0.10

^a QTL with same letter co-localized within the same genomic region

^b indicate QTL detected in Incognito et al. (2020)

^c PVE (%) = phenotypic variance explained (%), i.e., percentage of phenotypic variance explained by the QTL

^d The additive effects correspond to B73 allele

Trait	Chromosome	Position (cM)	One LOD interval (cM)	Co-located PQTLs ^a	Co-location between PQTLs and MT-QTLs detected in Incognito et al. (2020) ^b	Nearest marker	LOD	PVE (%) ^c	Additive effect ^d
VA _p	1	1.41	1.40–1.42			phi056	4.14	11.2	-0.26
LF _p	1	1.32	1.30–1.33			phi056	3.49	9.6	-0.13
	3	2.88	2.85–2.88			bnl8.15	2.66	7.4	-0.10
	5	1.28	1.27–1.28			UMC2301	5.94	15.7	-0.18
	5	1.37	1.36–1.38			UMC2301	3.73	10.2	-0.15
LFLl _p	1	2.20	2.16–2.26			phi056	2.04	5.7	0.10
	1	3.89	3.85–3.97			phi056	2.59	7.2	-0.11
	4	1.99	1.96–2.02		LL(4-2.21)	umc2278	2.18	6.1	-0.11
	4	2.76	2.75–2.80		LL(4-2.21)	ufg407-B11	2.61	7.2	0.10
	5	0.47	0.45–0.49			AY110625	3.49	9.5	-0.13
	8	0.34	0.30–0.36			csu332	2.48	6.9	-0.11
AZ _p	1	3.69	3.64–3.71			umc1566	3.05	8.4	0.11
	2	0.63	0.62–0.65			ZmISU53	4.28	11.6	-0.13
	2	0.73	0.71–0.76			ZmISU53	2.02	5.6	-0.10

^a QTL with same letter co-localized within the same genomic region

^b indicate QTL detected in Incognito et al. (2020)

^c PVE (%) = phenotypic variance explained (%), i.e., percentage of phenotypic variance explained by the QTL

^d The additive effects correspond to B73 allele

Trait	Chromosome	Position (cM)	One LOD interval (cM)	Co-located PQTLs ^a	Co-location between PQTLs and MT-QTLs detected in Incognito et al. (2020) ^b	Nearest marker	LOD	PVE (%) ^c	Additive effect ^d
	4	0.05	0.04–0.06			AY109715	2.23	6.2	-0.09
	9	1.15	1.14–1.15	d		umc1957	2.36	6.6	0.09
	9	1.22	1.21–1.23			umc1957	2.87	7.9	0.11
	10	1.21	1.20–1.23			mmpP4B06	3.33	9.1	0.11
EHPH _p	1	0.46	0.41–0.48			UMC1355	2.14	6.0	-0.09
	4	1.75	1.72–1.78		LL(4-2.21)	phi072	2.51	6.98	-0.11
	10	0.74	0.73–0.76			mmpP4B06	2.94	8.1	0.13
	10	0.81	0.80–0.84			mmpP4B06	2.90	8.1	0.12
	10	1.04	1.03–1.05			mmpP4B06	3.55	9.7	-0.14
EHP _p	3	0.37	0.34–0.42			bnl8.15	2.60	7.2	0.09
	4	1.87	1.86–1.89		LL(4-2.21)	phi072	4.38	11.8	-0.12
	8	0.57	0.56–0.60			csu332	2.31	6.4	-0.08
	9	1.05	1.05–1.06			umc1957	2.39	6.7	-0.09
	9	1.15	1.14–1.16	d		umc1957	4.88	13.1	-0.12

^a QTL with same letter co-localized within the same genomic region

^b indicate QTL detected in Incognito et al. (2020)

^c PVE (%) = phenotypic variance explained (%), i.e., percentage of phenotypic variance explained by the QTL

^d The additive effects correspond to B73 allele

Trait	Chromosome	Position (cM)	One LOD interval (cM)	Co-located PQTLs ^a	Co-location between PQTLs and MT-QTLs detected in Incognito et al. (2020) ^b	Nearest marker	LOD	PVE (%) ^c	Additive effect ^d
PH _p	1	2.09	2.07–2.15			phi056	2.95	8.1	-0.09
	3	0.55	0.53–0.63			bnl8.15	3.16	8.7	0.11
	3	1.07	1.00–1.10			bnl8.15	2.51	7.0	0.08
	4	2.06	2.04–2.09		LL(4-2.21)	umc2278	2.81	7.8	-0.09
	4	2.12	2.10–2.13		LL(4-2.21)	umc2278	3.08	8.5	-0.09
	5	1.82	1.79–1.88			UMC2301	2.22	6.2	-0.09
SD _p	6	0.39	0.39–0.40			umc2310	2.95	8.1	-0.12
	10	1.59	1.58–1.63			mmpP4B06	2.92	8.1	-0.12
^a QTL with same letter co-localized within the same genomic region									
^b indicate QTL detected in Incognito et al. (2020)									
^c PVE (%) = phenotypic variance explained (%), i.e., percentage of phenotypic variance explained by the QTL									
^d The additive effects correspond to B73 allele									

For LA_p and related traits, 5 to 7 QTLs were detected on chromosomes 3, 4, 5, 8, and 10 for LA_p and 2, 3, 5, 8, and 10 for LL_p accounting 6.1 to 10.6% of PP variation (Fig. 8 and Table 4). In nine out of 12 QTLs, B73 allele increased PP values. The QTLs for LA_p and LL_p on chromosome 3, 5, 8 (only the QTL detected at ca. 1.16 cM), and 10 were co-located and explained 8.1, 9.8, 7.4, and 6.3% of PP variance, respectively and changed PP values in 0.107, -0.123, 0.106, and 0.095 in average, respectively.

For LOV_p related traits and AZ_p, 1 QTL was detected for VA_p, 4 QTLs for LF_p, 6 QTLs for LFLL_p, and 7 QTLs for AZ_p, accounting for 11.2, 10.7, 7.1, and 7.9% of PP variance; respectively (Fig. 8 and Table 4). In the QTLs for VA_p and LF_p, and approximately in half of the detected QTLs for LFLL_p and AZ_p, B73 allele decreased PP values in 0.26, 0.142, 0.113, and 0.106; respectively. No co-locations between QTLs for LOV_p related traits were observed.

For PP of stem architecture traits, 18 QTLs were significant (Fig. 8 and Table 4). Among them, 5 QTLs were detected for EHPH_p, 5 for EH_p, 6 for PH_p, and 2 for SD_p, accounting for 7.76, 9.05, 7.71, and 8.11% of PP variance, respectively. In almost 70% of these QTLs, B73 allele decreased PP values. No co-locations between QTLs for PP of stem architecture traits were detected but one QTL for EH_p located at 1.15 cM on chromosome 9, co-located with one QTL for AZ_p.

Comparing the QTLs detected for PP of plant architecture traits with QTLs for the traits per se (Incognito et al. 2020), no co-localization was observed. One multi-trait QTL composed by QTLs of LFLL_p, EHPH_p, EH_p, PH_p co-located with one QTL for LL on chromosome 4 (Fig. 8 and Table 4).

4. Discussion

For decades, the main selection criteria among maize breeders were to improve grain yield and grain yield stability across environments, and the D used to select superior genotypes varied from 4 pl m⁻² in 1960's to 8 pl m⁻² in 1990's (Eyherabide et al. 1994). Moreover, during the last decades superior genotypes are tested at 16 pl m⁻² during the advanced phases prior to the commercialization (Lee and Tollenaar 2007). Thus, these breeding strategies have forced to select genotypes with compact plant type, and restricted vegetative and reproductive PP that would be the best physiological response to avoid bareness and grain yield penalties at high D (Haro et al. 2013). However, the paradigm that governed maize breeding during the last decades should change in the short term due to three current events: i) several regions of the world maize production area involve limiting environments in the supply of resources (Grassini et al. 2015; Dimes et al. 2015; Rodriguez et al. 2016; Rotili et al.), ii) the adoption of technology for seeding variable rates has increased specially in farms with high environmental variability (Melchiori and Garcia 2018), and iii) the current context of climate change and its impact on rainfalls (IPCC 2014) would generate environments that would become increasingly extreme and variable (Kusmec et al. 2017). Consequently, breeders are challenged to exploit PP (Monforte 2020) to develop high-yielding genotypes, capable of responding to contrasting supply of resources with high PP for traits related to resource capture and grain yield. Our study was focused on PP of plant architecture traits (i.e., those traits related to capture of aerial resources). Results showed a high variation in PP of these traits which would allow to select genotypes with contrasting PP for different target environments. The focus was not only placed on PP of architecture traits but also on the environmental modulation of the relationship between the trait per se and its PP. Such information would allow to improve genotypes for a collection of environments (de Felipe and Alvarez Prado 2021). Following this purpose, some plant architecture traits (AZ, EH, PH, EHPH, and SD) had a similar capacity (symmetrical) of response to PP under favorable (e.g. low D) and unfavorable (e.g. high D) environmental conditions, but others showed an asymmetrical response (LA, AV, LFLL). Interestingly symmetrical or asymmetrical responses of 90th and 10th percentile traits to their PPs may fit well with the better performance of plant architecture across environments. Thus, selection of lines with higher LA_p (asymmetrical response, with a higher LA response under low D than high D), AV_p (asymmetrical response, with more planophile leaf habit at low D but a erectophile leaf habit at high D), AZ_p (symmetrical response, with leaves close to 0° or 90° at low and high D; respectively) and EHPH_p (symmetrical response with higher and lower values at low and high D; respectively) seem to be possible. By contrast, selection of lines with high SD_p (symmetrical response) would be undesirable, especially for high D crops, because thinner stems could generate lodging (Flint-Garcia et al. 2003).

Some studies have postulated a negative relationship between the heritability of the trait per se and its PP, which would limit the efficiency of selection of both traits simultaneously. This hypothesis was not rejected for grain yield and grain yield components of several cereals (Sadras and Slafer 2012), and kernel weight in maize (Alvarez Prado et al. 2014), and was tested for leaf traits of several species including maize (Donovan et al. 2011). However, in our work this hypothesis was partially rejected since no relationship between heritability of the trait per se and PP was found for most traits with low PP, while a negative relationship was observed for two traits (SD and AZ) with PP above 0.84, i.e., those

traits strongly controlled by the environment. These differences could not be attributed to the approximation used to calculate heritability of traits per se, but to the number and type of trait and the methodologies for PP estimation (Finlay and Wilkinson 1963; Sadras et al. 2009, 2010). Moreover, comparing PP values of plant architecture traits obtained in this work, with PP values of kernel weight related traits using the same methodology for PP estimation (Alvarez Prado et al. 2014), we obtained higher PP values (maximum PP values of 0.96 vs 0.55).

Despite of a “plastic phenotype” was considered rather a nuisance initially (Bradshaw 1965), PP was lately (Bradshaw 2006) considered a trait per se with a complex genetic basis that can be selected to adapt genotypes to certain environments. Hence, studies of the genetic control of PP would be relevant. Some studies showed that in maize, the genetic control of several traits and their PPs were independent, e.g. foliar expansion (Reymond et al. 2003), kernel weight and its physiological determinants (Alvarez Prado et al. 2014) and several traits related to phenology, ear and plant morphology (Kusmec et al., 2017). We found that PP of plant architecture traits presented an independent genetic control of the trait per se, not rejecting the hypothesis postulated by Bradshaw (1965). This statement would also be supported by the low correlation values between the traits per se and their PPs and because no QTLs of PP of plant architecture traits co-located with QTLs for traits per se detected by Incognito et al. (2020) for the same RILs.

Regarding the study of genomic regions related to PP, some QTLs co-located, suggesting pleiotropy in the genetic control of PP of these traits. In three regions located at 2.27 cM of chromosome 5, at 1.16 cM of chromosome 8 and at 0.97 cM of chromosome 10, a QTL of LA_p co-located with one of LL_p, in contrast to the phenotypic relationships that indicate that LW was the most important trait by which plants regulate their LA (Sonohat and Bonhomme 1998 ; Incognito et al. 2020). The region located at 2.27 cM of chromosome 5 was the most important, because it explained a high percentage of variance explained (PVE) (9.8%) and because it contains genes directly involved in leaf growth such as *glossyN681A* (Neuffer and England) and leaf function as chloroplast RNA processing2 (Barkan et al. 1993), together with another gene that could indirectly affect LA regulation by intra-plant shading such as the *dwarf candidate6* (Todesco et al. 1990). Another QTL for LL_p located at 1.06 cM of chromosome 8 is of interest, since it explained 10.6% of PVE and contains the candidate gene *compact plant1* (Nelson Jr. and Ohlrogge 1961) that would proportionally reduce all vegetative organs of the plant.

For leaf orientation, an interesting QTL for AZ_p is the one located at 1.21 cM of chromosome 10, because it presented a high PVE (9.1%) and contains the candidate gene *dwarf candidate3685* (Winkler and Helentjaris 1993) that determine the elongation of plant organs mediated by the synthesis of gibberellin. Probably a change in the architecture of the plant promoted by gibberellin, such as twisting of leaf sheaths or of internodes triggered by the presence of neighbors could produce the reorientation of leaves towards inter-row spacing (Girardin and Tollenaar 1994), reducing shading among plants of the same row (Maddonna et al. 2001a). For LF_p, the QTL of greatest interest which presented the highest PVE (15.7%) of all the detected QTLs in this study, was the one located at 1.27 cM of chromosome 5. This QTL in addition to including the gene *glossyN681A* (Neuffer and England 1995) previously mentioned, would contain the gene *dwarf candidate6* (Todesco et al. 1990) and the *extended auricle1* (Osmont et al. 2003) that with a synergistic effect with the *liguleless1* (Becraft et al. 1990) and *liguleless2* (Walsh et al. 1998) would affect the establishment of the blade-sheath boundary potentially modifying the future growth of the leaf. Additionally, the region where a QTL was located with a high PVE (11.2%) for VA_p at 1.41 cM on chromosome 1, would constitute another region of interest containing the gene *humpback1* (Schneeberger et al. 1996). This gene would generate the proliferation of the sheath just below the auricle resulting in a bulging sheath that could potentially cause changes in the VA especially for leaves above of the ear node, with potential impact on carbon assimilation (Cagnola et al. 2021).

Finally, for the PP of stem architecture related traits, the QTL detected for EH_p at 1.15 cM on chromosome 9, generates the greatest interest because it presents a high PVE of 13.1% and because it is on a chromosome with the highest

density of QTLs for stem architecture associated traits found by Incognito et al. (2020) for the same population used in this study. Genes of interest that could affect EH_p were described in this region, like yellow-green2 (Neuffer and England 1995) and semaphore1 (Scanlon et al. 1996) which could produce shorter or brachytic plants, respectively, avoiding penalties on grain promoted by stalk lodging.

The study of the genetic bases of PP would strongly contribute to the success for future maize breeding in a rapidly changing environment (Monforte 2020). Although some causal genes controlling PP of traits have been studied, this field of research is in early stages (Laitinen and Nikoloski 2018). In addition to the availability of high-throughput genotyping technologies, new genomic tools together with the increasing use of automated phenotyping will help to increase knowledge about the genetic and molecular mechanisms underlying PP. In agreement to this, our results provide useful information about genomic regions involved in the PP of plant architecture traits in maize. More QTL analysis of PP on plant architecture traits using different genetic backgrounds are needed, in order to find stable QTLs capable of being used in marker assisted selection to develop genotypes with greater adaptation to environmental changes.

5. Conclusions

Our study gives information on PP of maize plant architecture traits, under contrasting environmental conditions. The independent genetic control could help breeders to jointly select for plant architecture traits per se and their PP. More studies are needed to relate PP of plant architecture traits with grain yield stability to an effective application of PP as a criterion in breeding programs. Moreover, the integration of climatic and soil information (environmental characterization) together with PP estimation, would help to select cultivars with PP plasticity of some plant architecture traits to changing environments.

Declarations

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Statements and Declarations

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Conflict of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

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Figures

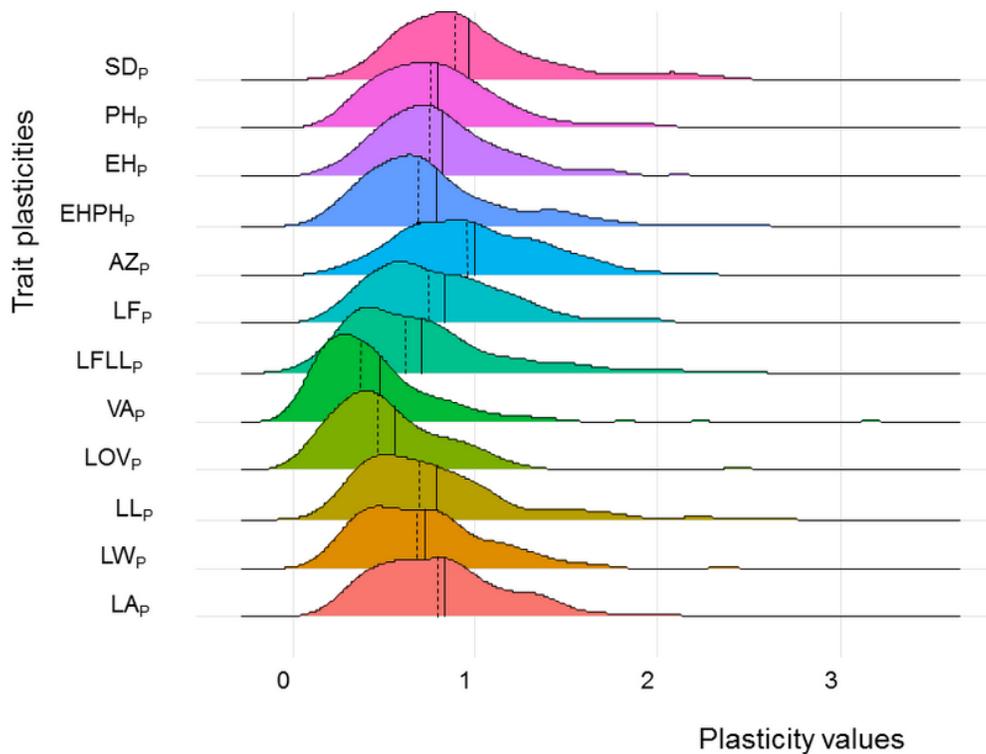


Figure 1

Distribution of phenotypic plasticity values of leaf area (LA_p), leaf width (LW_p), leaf length (LL_p), leaf orientation value (LOV_p), vertical angle (VA_p), relationship between leaf to flagging point (LF) and LL ($LFLL_p$), LF_p , azimuthal leaf orientation (AZ_p), relationship between ear height (EH) and plant height (PH) ($EHPH_p$), EH_p , PH_p , and stem diameter (SD_p) of 160 RILs from IBM B73 \times Mo17 Syn4 population. On each area, solid and dashed vertical lines indicate mean and median values of plasticity, respectively

Figure 2

Relationship between median of phenotypic plasticity (PP) and range, skew, and kurtosis of PP. The inset show the relationship between median of PP and coefficient of variation (CV) of PP

Figure 3

Relationship between broad-sense heritability and median of phenotypic plasticity (PP) of leaf and stem architecture traits in maize. a) linear and bi-linear regression adjusted to relationship between broad-sense heritability and PP to a data set composed by all evaluated traits. b) Parameter values of the bi-linear model fitted in a where a is the intercept,

b is the first slope, c indicates the PP value where a breaking point occurred and d indicates the second slope. Both heritability and PP are unitless

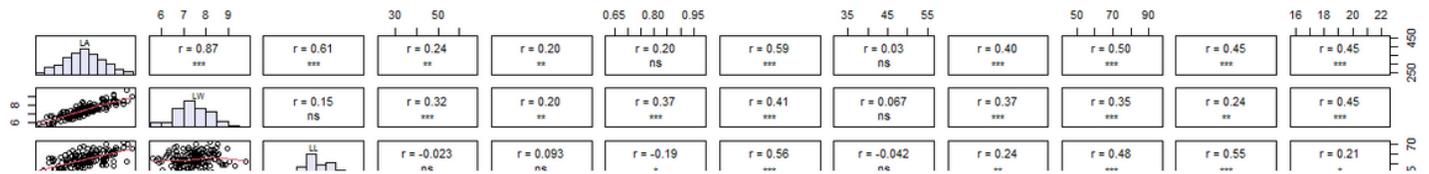


Figure 4

Phenotypic variation and correlation among traits for leaf area (LA), leaf width (LW), leaf length (LL), leaf orientation value (LOV), vertical angle (VA), ratio between leaf length to flagging point (LF) and LL (LFL), LF, azimuthal orientation (AZ), ratio between ear height (EH) and plant height (EHPH), EH, PH and stem diameter (SD). Bar charts show the frequency distributions of each trait on the diagonal. Pearson correlation values are above the diagonal with their corresponding P-values, and scatter plots are below the diagonal. Data correspond to mean values of 160 RILs from IBM B73 × Mo17 Syn4 population cultivated in four environments. The significance levels are indicated by symbols: * P < 0.05; ** P < 0.01; *** P < 0.001, ns: no significant

Figure 5

Relationship between leaf area-related traits and their plasticities under low intra-specific competition (90th percentile) and high intra-specific competition (10th percentile) conditions. (a, b) leaf area (LA), (c, d) leaf width (LW), (e, f) leaf length (LL). Each data set includes a total of 1920 data points (160 genotypes × 4 environments × 3 replications); percentiles were derived from twelve data points for each of the 160 genotypes (4 environments × 3 replications). In B, D, and F, dotted lines indicate y = 0; mean slope of regressions ± SE are also indicated. The significance levels are indicated by symbols: * P < 0.05; *** P < 0.001, ns: no significant difference

Figure 6

Relationship between leaf spatial distribution-related traits and their plasticities under low intra-specific competition (90th percentile) and high intra-specific competition (10th percentile) conditions. (a, b) leaf orientation value (LOV), (c, d) vertical angle (VA), (e, f) relationship between leaf flagging point (LF) and leaf length (LL) (LF/LL), (G, H) LF, (I, J) azimuthal orientation (AZ). Each data set includes a total of 1920 data points (160 genotypes × 4 environments × 3 replications); percentiles were derived from twelve data points for each of the 160 genotypes (4 environments × 3 replications). In b, d, f, h and j, dotted lines indicate $y = 0$; mean slope of regressions \pm SE are also indicated. The significance levels are indicated by symbols: *** $P < 0.001$, ns: no significant difference

Figure 7

Relationship between stem architecture-related traits and their plasticities under low intra-specific competition (90th percentile) and high intra-specific competition (10th percentile) conditions. (a, b) relationship between ear eight (EH) and plant height (PH) (EH/PH), (c, d) EH, (e, f) PH, (g, h) stem diameter (SD). Each data set includes a total of 1920 data points (160 genotypes × 4 environments × 3 replications); percentiles were derived from twelve data points for each of the 160 genotypes (4 environments × 3 replications). In b,d, f, and h, dotted lines indicate $y = 0$; mean slope of regressions \pm SE are also indicated. The significance levels are indicated by symbols: *** $P < 0.001$, ns: no significant difference

Figure 8

Quantitative trait loci (QTL) mapping results for plasticity of leaf area (LA_p), leaf width (LW_p), leaf length (LL_p), leaf orientation value (LOV_p), vertical angle (VA_p), relationship between leaf to flagging point (LF) and LL ($LFLL_p$), LF_p , azimuthal orientation (AZ_p), relationship between ear height (EH) and plant height (PH)($EHPH_p$), EH_p , PH_p , and stem diameter (SD_p) for 160 RILs from IBM B73 × Mo17 Syn4 population and for multi-trait QTL detected in Incognito et al. (2020) (MT per se)