

Heat stress in maize: characterization and phenotypic plasticity

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Abbreviations

CP, critical period for kernel set; Exp.n, experiment n; fPARI, fraction of incident photosynthetically active radiation intercepted by the canopy; HS, single hybrids; HSI, heat susceptibility index; L, inbred lines; NSE, non-stress environment; SE, heat stress environment. Other abbreviations are listed and described in detail in Table 2

Abstract

The future challenge will be to produce more maize and other crops, in stressed environments. Two experiments were carried out during the 2015-2016 season at INTA Leales field, Tucumán, Argentina. The treatments included a factorial arrangement of two thermal environments (non-stress and heat stress) and 15 hybrids (Exp.1) and 6 maize inbred lines (Exp.2). The hybrids and inbred lines showed phenotypic variability in most of the evaluated traits for heat stress during critical period for kernel set. The tropical genotypes (HS9, HS10 and L3) were identified as tolerant, while genotypes with a temperate x tropical and temperate genetic background (HS13, HS14 and L5) were identified as the most susceptible. There was a grain yield reduction of 82% and 78% in H13 and L5, respectively when comparing the non-heat stress environment with heat-stress environment. Range in phenotypic plasticity was similar for hybrids and inbred lines, being the largest for trait such as, grain yield, kernel number, anthesis-silking interval, harvest index, and the smallest for traits such as kernel weight, ear diameter, prolificacy, aboveground biomass at physiological maturity, cumulative thermal time to silking and leaf greenness post stress on ear leaf. The outcomes from this research are promising for future heat-stress screening, in order to increase the selection efficiency in a breeding program.

Introduction

There is evidence that average global temperatures are rising, global climate models predict increases in average temperature ranging between 1.8 and 5.8°C at the end of this century (IPCC, 2007). The future climate will also be affected by a greater variability in temperature and the increase in the frequency of hot days (Pittock, 2003). The world has the challenge of producing more maize, responsibly and sustainably, on the other hand the future crop production will be related to tolerance to high temperatures and drought (Sivakumar et al., 2005). Given this scenario, the future challenges of crop production in the tropics will be to produce more in low yielding environments (higher temperature, droughts, marginal soils, etc.), therefore greater emphasis should be placed on increasing grain yields of low-yielding areas.

Heat stress can be defined as a temperature rise above

a threshold value (generally 35°C) and for a sufficient period of time that causes irreversible damage to the plant growth and development (Tollenaar et al., 1979; Berry and Bjorkman, 1980; Wahid et al., 2007), although there may be a difference between temperate and tropical germplasm.

Current state of the art in the interpretation of maize grain yield determination under heat stress highlights the period between pollination and fertilization of the ovaries as the critical period (Cicchino et al., 2011) by reducing the main numerical component of the grain yield that is the kernel number (Rattalino Edreira and Otegui, 2012) which is highly associated with the plant and ear growth rate during the critical period for kernel set (Tollenaar et al., 1992; Andrade et al., 1999; Cicchino et al., 2010b; Rattalino Edreira and Otegui, 2012). According to several authors, heat stress affects the availability and viability of pollen (Schoper et al., 1986,

1987; Mitchell and Petolino, 1988). Pollen drying is a function of the air temperature and the viability decreases linearly with pollen dryness (Fonseca and Westgate, 2005). The temperate genotypes present a greater efficiency in the kernel set and greater partition of dry matter towards grain (Aluko et al., 1988; Andrade et al., 1996), however under heat stress during silking the advantage of the tropical genetic background seemed to be related to the reduction of kernel abortion (Rattalino Edreira et al., 2011) and the stable harvest index (Rattalino Edreira and Otegui, 2012). In the tropics, it is known that grain yield is limited by sink capacity (Goldsworthy, 1974). When this limitation occurs, according Andrade et al. (1996), breeding or crop management should focus, on the factors that allow increasing the kernel number per unit of area (crop growth rate, the partition to ears and the kernel number set per unit weight of ear around flowering).

The relationships between these traits have been thoroughly evaluated for hybrids grown under potential environments (Pagano and Maddonni, 2007) as well as in abiotic stress environments (Andrade et al., 2002; D'Andrea et al., 2006; Cicchino et al., 2010; Rossini et al., 2012; Rattalino Edreira and Otegui, 2013) however, the behavior of inbred lines has been much less documented (D'Andrea et al., 2006). Consequently, progress in our understanding of heritability in parent-progeny relationships (i.e., additive genetic effect) for the physiological and numerical determinants of grain yield has been poor, and even less in sub-tropical growing regions, such as northwestern Argentina (NOA), where heat stress can be important, since the monsoon regime exposes the crop to very high temperatures in part of their cycle.

The challenge for maize breeders has been the detection of successful combinations of inbred lines, aiming to reach maximum heterosis for grain yield (Duvick, 1999; Troyer, 2006) while preserving adequate resistance to biotic and abiotic stresses and other desirable agronomic traits. In the same way, combining both tropical and temperate grain yield generation strategies, could be relevant to increase the yields of NOA region.

It is widely accepted that the trait heritability decreases when phenotypic plasticity increases, due to environmental effects (D'Andrea et al., 2013). The phenotypic plasticity is inversely related to the predictive capacity of the inbred lines to form hybrids, this means that traits with high parental-progeny association (good predictor) have low phenotypic plasticity and vice versa (Sadras and Slafer, 2012). Therefore, it is interesting to evaluate the phenotypic plasticity of grain yield determinants in both hybrids and their inbred lines under non-stress and heat-stress environment and,

in this way, expand our knowledge in order to improve the future germplasm screening. This work aims to explore the phenotypic variability related to heat-stress tolerance during the critical period for kernel set and to quantify the phenotypic plasticity of agronomic traits in maize with different genetic backgrounds used by the INTA breeding program

Material and methods

Experimental design and treatments

Two experiments, one for inbred lines and one for hybrids were carried out during the 2015-2016 season at INTA Leales field, Tucumán, Argentina (27 ° 03 'S, 64 ° 15' O, 330 masl), on a homogeneous hapludol cumulic silty loam soil (Zuccardi et al., 1985). Each of these experiments was conducted in two neighboring independent thermal environments differentiated by daily maximum temperature reached during the critical period for kernel set. The thermal environments were generated in two greenhouses; inside each greenhouse a section for hybrids and one for inbred lines was separated. The treatments included a factorial arrangement of two thermal environments (non-stress and heat stress) and 15 maize hybrids (Exp.1) and 6 maize inbred lines (Exp.2). In each experiment the treatments were distributed in a randomized complete block design, with three repetitions in each thermal environment. The experimental unit was 7 m², two rows 5 m long spaced 0.7 m. Experiment were hand planted at three seeds per hill and thinned at V3 (Ritchie and Hanway, 1982) with a density of 6 plants m⁻² (suggested density for the region), the planting was staggered from 24/08/2015 to 03/09/2015 in order to coincide the flowering of the different genotypes.

Around each greenhouse two rows of borders were planted in order to ensure the presence of viable pollen inside the greenhouses. The experimental site was irrigated throughout the growing season by a drip irrigation system, keeping the soil near field capacity. All plots were fertilized with urea at V6 (Ritchie and Hanway, 1982) to a rate of 200 kg N ha⁻¹ and 80 kg P ha⁻¹ preplant. The crop was kept free of weeds, insects and diseases through chemical and manual controls.

Thermal environments

With the use of two metallic structures covered with polyethylene (greenhouses) two levels of maximum daily temperatures were generated during the critical period for kernel set: non stress environment –NSE- (T < 35°C) and heat stress environment –SE- (T > 35°C), since it was considered as heat stress a temperature above 35°C at the ear level for at least 1 hour (Barnabás et al., 2008). The SE level consisted in covering a

greenhouse of 500 m² with a plastic LTD of 200 μ (25% attenuation of the incident radiation) around flowering (7 days before and 7 days after R1). The increase in temperature began when 50% of the plants in the plots of each cultivar reached approximately V16 (Ritchie and Hanway, 1982) and finished 7 days after the start of silking. The NSE level consisted in opening the sides and doors of the greenhouse. Once the CP was finished, the plastic was removed. Both greenhouses were covered with plastic at sowing in order to increase the soil temperature and thus allow a uniform germination of the different cultivars. Hourly air temperatures were recorded with 2 sensors inside each greenhouse at the main ear height and connected to data loggers (Brand: ETI, Model: thermadata logger).

Genetic material

Four tropical maize inbred lines (L) of the INTA Leales breeding program (L1, L2, L3, L4), 2 temperate maize inbred lines of the EEA INTA Pergamino breeding

program (L5, L6) and 15 simple hybrids (HS) were used. The hybrids resulting from partial diallel crosses between inbred lines without reciprocals (Table 1). The diallel crosses were made in the previous season trials (2014-2015). Inbred lines were selected for showing different degrees of adaptation to contrasting thermal environments (F. Canteros and R. Lorea, personal communication 02/06/2014), determined visually (without being quantified).

Measurements

The traits quantified (Table 2) with their respective form of measurement were:

Grain yield and yield components

At physiological maturity the present ears of 2 m² of the central part of the plot were hand harvested and shelled to determine grain yield (GY) expressed on dry weight basis. Kernel number (KN) was determined indirectly by the grain yield / kernel weight ratio. Three

Table 1 - Germplasm with their pedigrees involved in the study, diallel cross pattern and heat susceptibility index and percentage of grain yield decrease across thermal environments. L: inbred lines, HS: hybrids, HSI: heat stress index, %GY-reduction: percentage of grain yield decrease under heat stress respect to non-stress environment.

					HSI	%GY-reduction	
Inbred lines	L1	Genetic Background	Tropical	Pedigree	TUXPEÑO/ETO	1.23	57.06
	L2		Tropical		TUXPEÑO/ETO	1.63	75.20
	L3		Tropical		EA1669c (TUXPEÑO/ETO)	-0.02	-0.74
	L4		Tropical		TUXPEÑO/ETO	0.96	44.79
	L5		Temperate		LP562 (R49022 x M370)	1.68	77.62
	L6		Temperate		LP598 (F2 ACA 2000)	0.93	43.02
Hybrids	HS7	Diallel Cross:	♀L2 X ♂L1			0.69	31.52
	HS8		♀L3 X ♂L1			0.80	36.90
	HS9		♀L3 X ♂L2			0.50	23.11
	HS10		♀L4 X ♂L1			0.27	12.57
	HS11		♀L4 X ♂L2			0.76	35.05
	HS12		♀L4 X ♂L3			0.81	37.21
	HS13		♀L5 X ♂L1			1.78	81.61
	HS14		♀L5 X ♂L2			1.56	71.56
	HS15		♀L5 X ♂L3			1.29	59.08
	HS16		♀L5 X ♂L4			1.25	57.15
	HS17		♀L6 X ♂L1			0.87	39.86
	HS18		♀L6 X ♂L2			1.21	55.67
	HS19		♀L6 X ♂L3				
	HS20		♀L6 X ♂L4				
	HS21		♀L6 X ♂L5				

Table 2 - Abbreviation and description of evaluated traits.

Abbreviation	Trait description
ASI	anthesis-silking interval
Biomass_pm	aboveground biomass at physiological maturity (kg.m-2)
Biomass_post	aboveground biomass post stress (kg.m-2)
Biomass_pre	aboveground biomass pre stress (kg.m-2)
CGR	crop growth rate (g.m-2.d-1)
CGR_cp	crop growth rate during critical period (g.m-2.d-1)
CGR_fill	crop growth rate during effective grain filling (g.m-2.d-1)
Diftemp	difference between the leaf temperature and the environmental temperature (°C)
ED	ear diameter (mm)
EL	ear length (mm)
fPARi	fraction of incident photosynthetically active radiation intercepted by the canopy
GY	grain yield (kg.ha-1)
HI	harvest index (%)
KN	kernel number per m2
KW	thousand kernel weight (g)
Prol	prolificacy (n°ears.pl-1)
R1	thermal time to silking (°Cd)
R6	thermal time to physiological maturity (°Cd)
SPAD_post	SPAD value post stress
SPAD_postear	SPAD value post stress on ear leaf
SPAD_postflag	SPAD value post stress on flag leaf
VT	thermal time to tasseling (°Cd)

samples of 200 kernels per plot were taken, dried in an oven at 90°C until constant weight, to determine the thousand kernel weight (KW). The Prolificacy (Prol) was calculated based on the total of ears harvested per plant at physiological maturity, all ears with at least one kernel set were considered. To determine the ear diameter (ED), the central portion of 5 representative ears of each plot were measured at harvest with a digital caliber (Brand: Blue point MCAL6A).

Eco-physiological components of yield

The fraction of incident photosynthetically active radiation intercepted by the canopy (fPARi) was calculated from PAR measured above the canopy and PAR measured below the green leaves but above the senesced leaves at the bottom of the canopy. The fPARi was determined weekly throughout the cycle using a linear sensor (LI-COR, Lincoln, Nebraska). Measurements were made between 12 and 14 h in diaphanous days

placing the sensor perpendicular to the rows, being completely covered by the two rows following the methodology of Gallo and Daughtry (1986).

To determine aboveground Biomass, destructive samplings of five consecutive plants per plot were taken in three moments: before the start of stress (Biomass_pre), at the end of stress (Biomass_post) and at physiological maturity (black layer visible on the kernel of the middle portion of the ear) (Biomass_pm). In each sampling the plants were cut at ground level, taken to a forced air circulation oven at 60°C until constant weight and weighed.

Crop growth rate during CP (CGR_cp) was estimated from the determined biomass values (at V14 and R2) by means of the relationship between the biomass accumulated by the crop (in g m-2) and the time elapsed (in days) in this period. The harvest index (HI) was calculated as the ratio between grain yield per m2 and aboveground biomass per m2 of the crop at physiological maturity on a dry weigh basis

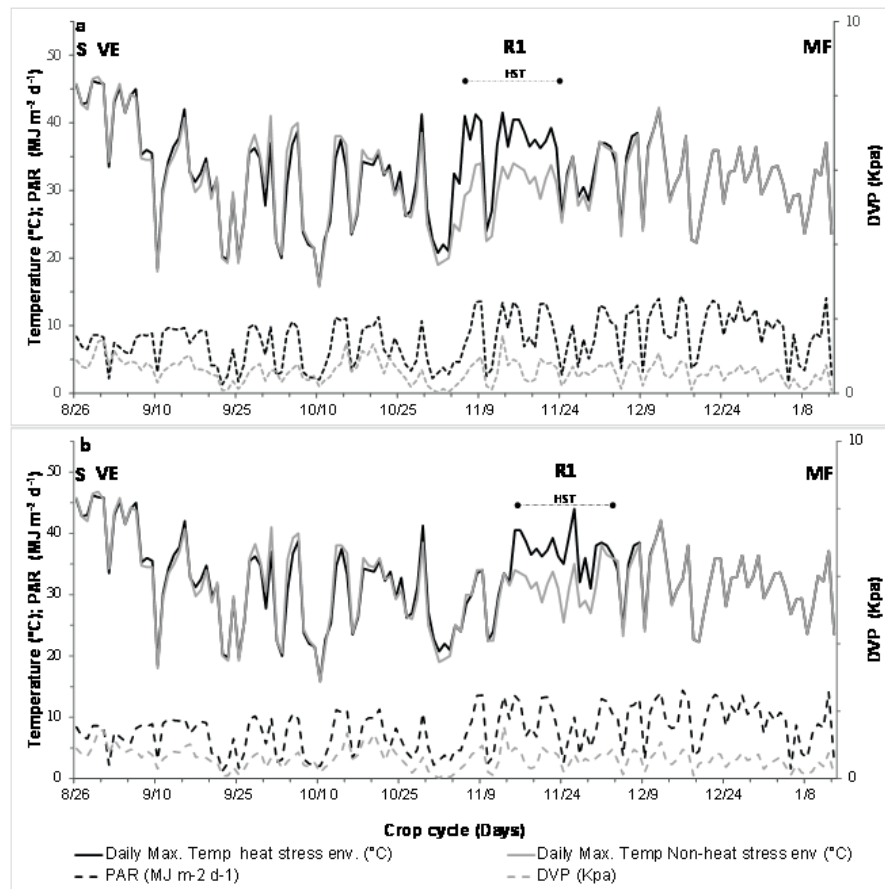


Fig. 1 - Daily maximum temperature evolution at ear level of heat stress (filled black line) and non-stress environment (filled grey line), daily incident photosynthetically active radiation (dotted black line) and vapor pressure deficit - VPD (dotted grey line) during the crop cycle for maize hybrids (a) and parental inbred lines (b). HST represent the length of the heating period. S: sowing date; VE: emergency date; R1: silking; MF: physiological maturity.

Status indicators

Leaf greenness measurements were made post stress (SPAD_{post}) with SPAD (Minolta) on flag leaf (SPAD_{postflag}) and ear leaf (SPAD_{postear}) on three plants per plot. Leaf rolling scores (1= without leaf rolling, 5= full leaf rolling) were determined during the stress period following the methodology of Bänziger et al. (2000). Leaf temperature in flag leaf was determined in three plants per plot with the use of an infrared thermometer (CEM Infrared Thermometer DT-810) during the stress period following the methodology used by Nielsen and Anderson (1989). The data was taken between 12 and 14 h, placing the thermometer at constant distance of approximately 20 cm and constant angle. Simultaneously, air temperature was recorded by sensors located 1.2 m height. With leaf temperature and ambient temperature, a new variable was calculated, which consisted in the difference between the leaf temperature and the environmental temperature (Diftemp).

Phenological variables

Thermal time (TT) were determined from emergency to VT (VT), emergency to R1 (R1) and emergency to R6 (MF). VT and R1 were considered when 50% of the plants of each plot reached anthesis and silking, respectively. The anthesis-silking interval (ASI) was calculated by the difference R1-VT. Thermal time accumulation was calculated according to Muchow (1990), using 10°C as the base temperature (Lindquist et al. 2005).

Statistical analysis

Statistical analyzes were carried out with the Infostat program (Di Rienzo et al., 2018). The analysis of variance (ANOVA) was performed to evaluate the effects of genotype, thermal environment and its interaction on each of the traits. To determine significant differences ($p < 0.05$) between the means, the formation of excluding groups test (DGC) was applied (Di Rienzo et al., 2002). An ANOVA for a factorial design was adjusted, with the effect of replications nested in thermal environment level.

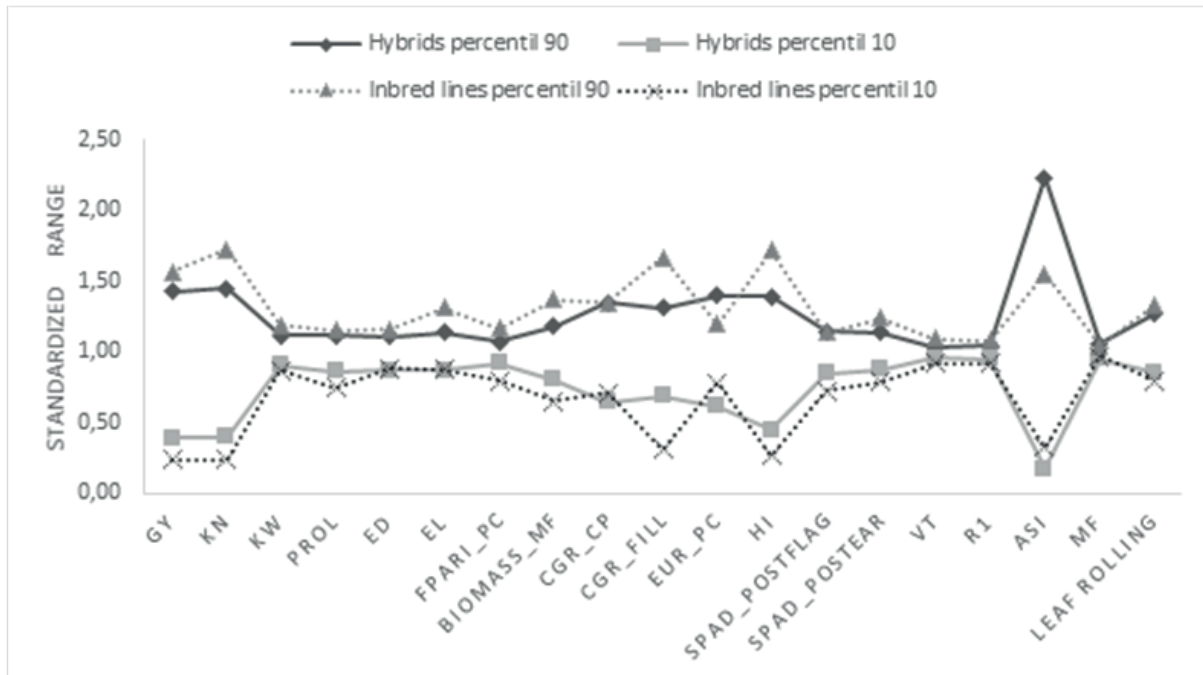


Fig. 2 - Phenotypic plasticity of traits (listed in table 2) measured in two thermal environments (non-stress and heat stress) in 6 maize inbred lines and 15 derived hybrids. The median is set to 1, and the 10th and 90th percentiles are expressed as ratios with respect to the median value.

Model: $Y_{ijk} = \mu + G_i + T_j + T_j > R_k + (GT)_{ij} + E_{ijk}$ (2.1)

where, Y_{ijk} is the response variable, μ is the overall mean, G effect of the genotype, T the effect of the thermal environment, $T_j > R$ is the effect of the replication within thermal environment, $(GT)_{ij}$ is the effect of the genotype and thermal environment interaction and E the random error.

Leaf rolling trait was analyzed using the nonparametric method of Kruskal Wallis.

The tolerance to heat was calculated with a heat susceptibility index (HSI) for each maize hybrid and inbred line using the equation (2.2) of Fischer and Maurer (1978), it takes into account the grain yield in stress vs. non stress environment.

$$HSI = (1 - Y_h / Y) / (1 - X_h / X) \quad (2.2)$$

where, Y_h and Y are the phenotypic means of grain yield for each genotype under heat stress environment and non-stress environment, respectively, and X_h and X are the phenotypic means of grain yield for all the genotypes under heat stress environment and non-stress environment, respectively.

The phenotypic plasticity was determined for the evaluated traits; each variable was normalized for a common comparison of both hybrids and inbred lines (Sadras and Slafer, 2012). For this, the 50th percentiles (median), 10th and 90th percentiles were obtained for each genotype (6 inbred lines and 15 hybrids) and then

averaged within each group. The median value was set at 1, and the 10th and 90th percentiles were expressed proportional to the median for each trait.

Results and Discussion

Two thermal environments generated by the greenhouses were differentiated by the maximum daily temperatures reached around R1, both in hybrids (Fig. 1A) and inbred lines (Fig. 1B). In both experiments, the heating period was of about 15 days around R1. In hybrids it occurred between November 06 and 22, whereas in inbred lines it occurred between November 15 and December 1. The sowing split concentrated the silking of hybrids and inbred lines in approximately 5 days (from November 11 to 16 and from November 22 to 26, respectively) within the heat stress period. The gradual increase of temperature generated in the heat stress environment was reasonable in the maximum values reached; the heating system simulated temperatures likely to be reached on hot days in subtropical regions. This is important since the heat stress effect depends on the magnitude of maximum temperature imposed and also on the rate of temperature change (Crafts-Brandner and Salvucci, 2002; Wahid et al., 2007).

The vast majority of heat stress research focused on biochemical and molecular responses using only a limited number of genotypes with stress applied in vitro or has been conducted in field conditions on single hybrids maize for high production areas (Mayer et al.,

Table 3 - Grain yield (GY), kernel number (KN), kernel weight (KW), prolificacy (Prol), ear diameter (ED) and ear length (EL) for 15 maize hybrids (HS) subjected to contrasting thermal environments (NSE and SE). ANOVA results are presented at the bottom of the table.

Genotype	GY (kg.ha ⁻¹)		KN (granos.m ⁻²)		KW (g)		Prol (n°ears.pl ⁻¹)		ED (mm)		EL (mm)	
	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE
HS7	7188.95 b A	4922.93 a B	2377.73 b A	1486.92 a B	302.37 c	335.20 b	1.13	1.27 a	43.40 b A	35.65 b B	128.87 a	129.00 a
HS8	11272.08 a A	7113.20 a B	3261.10 a A	1925.70 a B	345.76 b	366.30 a	1.00	1.00 b	47.39 a A	46.49 a A	150.59 a	157.62 a
HS9	9836.23 a A	7563.08 a A	3120.38 a A	2360.49 a B	315.28 c	323.33 b	1.07	1.13 b	46.56 a A	44.52 a A	141.41 a	151.81 a
HS10	7193.14 b A	6289.22 a A	2327.61 b A	1982.15 a A	309.00 c	316.54 b	1.00	1.13 b	46.36 a A	42.43 a A	130.51 a	136.27 a
HS11	8500.38 b A	5520.61 a B	2813.52 b A	1824.42 a B	301.40 c	306.20 b	1.13	1.33 a	44.73 b A	42.52 a A	140.05 a	142.05 a
HS12	7676.71 b A	4819.88 a B	2530.87 b A	1706.31 a B	303.37 c	285.24 c	1.00	1.13 b	48.23 a A	45.69 a A	120.35 a	136.69 a
HS13	8062.23 b A	1482.40 b B	2240.59 b A	421.41 b B	363.55 a	351.80 a	1.00	1.00 b	46.20 a A	25.79 d B	149.13 a	130.61 a
HS14	8283.66 b A	2356.14 b B	2564.50 b A	755.10 b B	322.34 b	310.60 b	1.00	0.87 b	43.41 b A	38.04 b A	132.11 a	116.36 b
HS15	6889.22 b A	2819.30 b B	2060.88 b A	856.54 b B	332.55 b	325.61 b	1.00	1.07 b	44.66 b A	41.66 a A	129.26 a	103.99 b
HS16	8082.07 b A	3463.49 b B	2504.00 b A	1104.58 b B	322.73 b	314.38 b	1.00	0.93 b	45.71 a A	36.53 b B	141.18 a	134.58 a
HS17	8351.54 b A	5023.01 a B	2449.39 b A	1430.63 a B	341.30 b	353.26 a	1.00	1.07 b	43.99 b A	41.38 a A	127.25 a	152.61 a
HS18	7238.27 b A	3208.45 b B	2389.60 b A	1106.09 b B	303.60 c	291.11 c	0.93	1.00 b	43.71 b A	36.95 b B	135.42 a	128.31 a
HS19	6289.71 b A	3388.49 b B	2089.00 b A	1220.03 b B	301.86 c	276.02 c	1.00	1.13 b	42.56 b A	39.34 b A	128.38 a	130.28 a
HS20	7683.39 b A	2949.65 b B	2660.57 b A	1029.51 b B	289.94 c	283.82 c	1.00	0.87 b	44.88 b A	36.54 b B	138.92 a	151.09 a
HS21	1630.04 c A	889.61 b B	534.65 c A	316.10 b A	302.24 c	279.53 c	0.67	0.47 c	39.47 c A	30.59 c B	105.07 b	79.18 c
Means	7611.84 A	4120.63 B	2394.96 A	1301.73 B	317.15 A	314.60 A	1.00 A	1.03 A	44.71 A	39.16 B	132.90 A	133.29 A
Shapiro-Wilks	ns		ns		ns		ns		ns		ns	
Thermal Env.	0.0011**		0.0005**		0.7125		0.5766		0.0007**		0.9225	
Genotype	<0.0001**		<0.0001**		<0.0001**		<0.0001**		<0.0001**		<0.0001**	
Thermal Env.>block	0.0366*		0.1647		0.002**		0.0252*		0.1649		0.0576	
Genotype* Thermal Env	0.0027**		0.0201*		0.0267*		0.4092		<0.0001**		0.0098**	

Means, multiple comparisons test DGC, normality test and level of significance for treatment effect and their interaction. GY: grain yield, KN: kernel number, KW: kernel weight, prol: prolificacy, ES: eardiameter, LE: ear length. NSE: non-stress environment in critical period, SE: stress- environment in critical period. Means with the same lowercase letter are not significantly different ($p > 0.05$) within each thermal environment, in the characters that are detailed with tiny letters only one thermal environment they correspond to the average of each genotype across the environments. Means with the same capital letter are not significantly different ($p > 0.05$) between NSE and SE level.

2012, Rattalino et al. 2014, Neiff et al., 2016). Therefore, limited breeding progress has been made in the development of improved maize germplasm with specific tolerance to elevated temperatures. Include both hybrids and their parental inbred lines in the research would allow progress in our understanding of the heritability in parent-progeny relationships (i.e., additive genetic effect) for the physiological and numerical determinants of grain yield for heat stress conditions

Grain Yield and its numerical components

It has been observed that GY and KN of maize hybrids are highly sensitive to heat stress at critical period for kernel set; however, the effect of the stress is highly dependent on the genetic background. In heat stress environment, tropical hybrids (HS7, HS8, HS9, HS10,

HS11 and HS12) showed the highest GY, differing significantly from those with temperate x tropical and temperate genetic background (Table 3). The hybrid HS21, formed by the combination of two temperate inbred lines, showed the lowest GY in both environments, probably due to limited adaptation. Hybrids HS9 and HS10 maintained its GY and KN stable across thermal environments, therefore, these hybrids behaved as tolerant to heat stress. In addition, HS8 was highlighted, being the highest yielding in non-stress environment and the second more yielding under stress environment. On the contrary, HS13 showed the highest grain yield reduction across environments (8062.23 vs 1482.4 kg ha⁻¹), being the most susceptible to heat stress. Among the principal causes of the GY decrease, those related to the availability and viability of pollen were discarded since the stigmas of each plant in heat stress envi-

Table 4 - Grain yield (GY), kernel number (KN), kernel weight (KW), prolificacy (Prol), ear diameter (ED) and ear length (EL) for 6 maize inbred lines (L) subjected to contrasting thermal environments (NSE and SE). ANOVA results are presented at the bottom of the table.

Genotype	GY (kg.ha ⁻¹)		KN (granos.m ⁻²)		KW (g)		Prol (n°ears.pl ⁻¹)		ED (mm)		EL (mm)	
	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE
L1	5146.73 a A	2209.79 a B	1738.92	682.51 a	300.74	317.63 a	1.03 A	1.13 A	41.24	35.22 b	134.29 a	135.59 a
L2	1817.41 c A	450.61 b B	663.20	173.32 b	274.89	259.87 b	1.20 A	0.60 B	38.03	31.55 c	117.41 b	91.98 b
L3	2739.30 b A	2759.65 a A	1039.68	1043.88 a	263.34	264.64 b	1.00 A	0.97 A	42.05	41.30 a	92.80 c	88.48 b
L4	2713.44 b A	1498.18 a B	1282.82	651.78 a	217.48	230.60 c	1.17 A	1.03 A	36.62	34.09 c	83.98 c	95.27 b
L5	1124.79 c A	251.71 b B	483.65	133.84 b	232.56	201.77 c	1.04 A	0.73 B	34.75	25.16 d	94.62 c	89.83 b
L6	3478.06 b A	1981.91 a B	1501.51	892.97 a	230.60	220.65 c	1.14 A	1.10 A	35.45	32.20 c	94.28 c	97.90 b
Means	2836.62 A	1525.30 B	1118.56 A	578.51 B	253.27 A	249.19 A	1.10 A	0.93 B	38.03 A	33.08 B	102.73 A	99.92 A
Shapiro-Wilks	Ns		ns		ns		ns		ns		ns	
Thermal Env.	0.0259*		0.0346*		0.3406		0.0138*		0.0119*		0.6601	
Genotype	<0.0001**		<0.0001**		<0.0001**		0.0554		<0.0001**		<0.0001**	
Thermal Env.>bloque	0.0523		0.0273*		0.9027		0.5145		0.1875		0.0201*	
Genotype* Thermal Env	0.0405*		0.0694		0.4550		0.0144*		0.0612		0.0066**	

Means, multiple comparisons test DGC, normality test and level of significance for treatment effect and their interaction. GY: grain yield, KN: kernel number, KW: kernel weight, prol: prolificacy, ES: ear diameter, LE: ear length. NSE: non-stress environment in critical period, SE: stress- environment in critical period. Means with the same lowercase letter are not significantly different ($p > 0.05$) within each thermal environment, in the characters that are detailed with tiny letters only one thermal environment they correspond to the average of each genotype across the environments. Means with the same capital letter are not significantly different ($p > 0.05$) between NSE and SE level.

ronment had available fresh pollen provided by border plants. In fact, the confused effect that could generate a poor availability of pollen in the differential sensitivity of genotypes to heat stress, could be discarded since there was no relationship between GY and R1 under stress environment both in hybrids ($GY = 4755.77 - 0.8 R1$; $R2 = 0.0001$; $p\text{-valor} = 0.9$) and inbred lines ($GY = 4488.85 - 3.16 R1$; $R2 = 0.04$; $p\text{-valor} = 0.4$) (data not shown). In this way, it could be assumed that the principal cause of GY reduction due to heat stress during the critical period for kernel set was the kernel abortion, in agreement with Rattalino Edreira and Otegui (2012), being higher in genotypes with tempered genetic background.

In general, inbred lines showed lower GY under heat stress environment respect to non-stress environment, with the exception of L3, which maintained GY stable across environments (Table 4). In heat stress environment, L1, L3, L4, and L6 showed the highest GY, however, L2 and L5 showed the lowest ones. There was a significant effect of G and T on KN in inbred lines (Table 4). The heat stress affected KN in most of the inbred lines, with average values ranging from 578.51 to 1118.56 kernels m⁻² across environments. The inbred line L3 showed high tolerance to heat stress, since its KN was not affected across thermal environments. There was no evidence of any increase in KW (both in hybrids and inbred lines) that compensated, at least

partially, the large reduction in KN produced by heat stress during the critical period for kernel set. This result is in agreement with other authors working under heat stress (Rattalino Edreira et al., 2014; Ordóñez et al., 2015) and drought (Lu et al., 2011) indicating that KW is a very stable trait across environments. Although, a KW increase tendency has been observed in tropical genotypes under heat stress environment.

According to Suwa et al. (2010), high temperatures reduce ear expansion by altering hemicellulose and cellulose synthesis through reduced supply of photosynthates. The hybrid with the greatest GY decrease across environments (HS13) presented the greatest drop in the ED. The inbred line L3 kept GY and ED stable across thermal environments.

There was different response of prolificacy to heat stress effect both in hybrids and inbred lines, in agreement with Hussain et al. (2006). There was lower prolificacy in temperate hybrid than tropical and temperate x tropical hybrids genetic background. Hybrid HS21 presented the lowest prolificacy, which could imply a limited adaptation to the area, while HS7 and HS11 (both formed by tropical inbred lines) showed the highest prolificacy. These hybrids, highly prolific, showed significant KN reduction across thermal environments, meaning that the second ear could not compensate the KN decrease under stress. In inbred lines, there was a significant prolificacy decrease in L2 and L5 under heat

Table 5 - Aboveground biomass at physiological maturity (Biomass_pm), crop growth rate during critical period (CGR_cp), harvest index (HI), SPAD value post stress on flag leaf (SPAD_postflag), SPAD value post stress on ear leaf (SPAD_postear), thermal time to tasseling (VT), thermal time to silking (R1) and anthesis-silking interval (ASI) for 15 maize hybrids subjected to contrasting thermal environments (NSE and SE). ANOVA results are presented at the bottom of the table.

Genotype	Biomass_pm (kg.m ⁻²)		CGR_cp (g.m ⁻² .d ⁻¹)		HI (%)		SPAD_postflag		SPAD_postear		VT		R1		ASI	
	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE
HS7	2.13	1.88 c	42.24	18.74	33.75 a A	26.21 a A	40.50 c A	34.18 a A	41.94 b	739.06 b	758.79 a	773.24 a A	814.40 b A	34.19 a	55.61 b	
HS8	2.84	2.37 a	26.81	26.88	39.69 a A	30.01 a A	41.05 c A	31.55 a B	38.92 b	699.59 c	748.63 a	715.45 b A	753.44 b A	15.87 b	4.81 c	
HS9	2.35	2.12 b	25.79	17.14	41.86 a A	35.65 a A	37.34 c A	36.86 a A	40.22 b	761.99 a	779.42 a	754.71 a A	795.85 b A	0.00 b	16.81 c	
HS10	1.76	1.92 c	29.50	14.26	40.89 a A	32.76 a A	44.19 b A	43.56 a A	43.13 b	716.31 b	743.83 a	758.62 a A	801.15 b A	42.32 a	57.32 b	
HS11	2.11	1.84 c	28.12	14.05	40.29 a A	29.91 a A	43.40 b A	44.44 a A	45.87 b	724.00 b	772.42 a	746.72 a A	803.24 b A	22.72 b	30.70 c	
HS12	2.03	1.94 c	21.89	20.93	37.83 a A	24.84 a B	42.46 b A	36.89 a B	39.09 b	707.01 c	714.68 b	716.31 b A	714.68 c A	9.30 b	0.00 c	
HS13	2.26	1.65 c	31.42	22.46	35.67 a A	8.97 b B	56.12 a A	42.19 a B	43.00 b	764.01 a	768.24 a	777.81 a A	768.26 b A	13.80 b	0.00 c	
HS14	2.27	1.70 c	31.06	19.12	36.39 a A	13.87 b B	46.01 b A	39.85 a A	50.30 a	766.64 a	760.12 a	779.60 a A	776.24 b A	13.55 b	16.12 c	
HS15	1.89	1.57 d	26.34	19.39	36.41 a A	17.95 a B	43.83 b A	39.20 a A	48.96	769.37 a	762.15 a	756.79 a A	777.68 b A	0.00 b	15.54 c	
HS16	1.98	1.79 c	22.39	15.19	40.85 a A	19.35 a B	46.34 b A	45.32 a A	42.53	767.86 a	757.63 a	790.39 a A	774.46 b A	22.53 b	16.82 c	
HS17	2.24	1.99 b	37.73	15.49	37.29 a A	25.29 a B	45.78 b A	32.94 a B	42.52 b	751.48 a	779.63 a	783.77 a A	786.84 b A	32.29 a	7.22 b	
HS18	2.11	1.60 c	28.00	17.33	34.30 a A	20.05 a B	39.73 c A	33.93 a A	37.02 b	738.64 b	772.42 a	770.24 b A	834.92 a A	31.60 a	52.34 b	
HS19	1.91	1.39 d	33.05	15.00	32.93 a A	24.38 a A	35.89 c A	26.95 b B	45.32	726.72 b	771.32 a	734.32 b B	808.54 b A	7.60 b	37.22 b	
HS20	1.98	1.70 c	19.71	19.49	38.83 a A	16.35 a B	36.01 c A	37.53 a A	37.53 b	734.51 b	748.99 a	750.85 a A	786.84 b A	16.33 b	38.42 c	
HS21	1.24	1.16 e	23.38	15.27	13.15 b A	7.67 b B	36.01 c A	39.83 a A	40.53 b	734.51 b	755.97 a	775.00 a B	856.76 a A	40.49 a	101.82 a	
Means	2.07 A	1.77 B	28.49 A	18.05 B	36.01 A	22.29 B	42.26 A	37.81 B	41.62 B	738.99 A	756.46 A	758.49 B	788.79 A	21.72 A	28.66 A	
Shapiro-Wilks	ns		ns		ns		ns		ns		ns		ns		ns	
Thermal Env.	0.0074**		0.0019**		0.0024**		0.0001**		0.0032**		0.0998		0.0204*		0.2831	
Genotype	<0.0001**		0.9076		<0.0001**		<0.0001**		0.0001**		<0.0001**		<0.0001**		<0.0001**	
Thermal Env.>block	0.0804		0.8298		0.0191*		0.9742		0.4519		0.0001**		0.0129*		0.0008**	
Genotype* Thermal Env.	0.0581		0.8325		0.0089**		0.0089**		0.2551		0.0181*		0.0009**		0.0001**	

Means, multiple comparisons test DGC, normality test and level of significance for treatment effect and their interaction. NSE: non-stress environment during critical period, SE: stress- environment during critical period. Means with the same lowercase letter are not significantly different ($p > 0.05$) within each thermal environment. Traits that are detailed with tiny letters only one thermal environment corresponds to the average of each genotype across environments. Means with the same capital letter are not significantly different ($p > 0.05$) between NSE and SE level.

Table 6 - Aboveground biomass at physiological maturity (Biomass_pm), crop growth rate during critical period (CGR_cp), harvest index (HI), SPAD value post stress on flag leaf (SPAD_postflag), SPAD value post stress on ear leaf (SPAD_postear), thermal time to tasseling (VT), thermal time to silking (R1) and anthesis-silking interval (ASI) for 6 maize inbred lines subjected to contrasting thermal environments (NSE and SE). ANOVA results are presented at the bottom of the table

Genotype	Biomass_pm (kg.m ⁻³)		CGR_cp (g.m ⁻² .d ⁻¹)		HI (%)		SPAD_postflag		SPAD_postear		VT		R1		ASI	
	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE	NSE	SE
L1	1.33	1.08 a	13.38 a	19.29 a	38.7	20.45 a	36.58	38.94 a	45.31	41.08 a	935.32	932.02 b	958.21	1002.10 b	22.89 b	70.08 a
L2	1.41	1.10 a	13.57 a	16.72 a	12.89	4.13 b	36.95	31.33 a	40.78	35.99 a	827.71	877.38 c	873.53	922.44 c	45.82 a	45.06 a
L3	1.04	1.12 b	11.23 a	12.49 b	26.38	24.69 a	34.43	31.04 a	28.68	34.24 b	802.25	826.18 d	856.42	867.34 d	54.18 a	41.17 a
L4	0.89	0.75 c	7.89 b	13.27 b	30.49	19.98 a	35.52	33.92 a	32.00	33.72 b	837.34	830.63 d	856.42	868.47 d	19.08 b	37.85 a
L5	0.61	0.48 d	11.39 a	8.69 c	18.41	5.24 b	31.21	35.66 a	26.50	27.86 b	943.31	965.78 b	943.31	1007.00 b	0.00 b	41.22 a
L6	0.90	0.79 c	8.61 b	9.76 c	38.67	25.09 a	21.42	22.60 b	24.47	26.05 b	981.4	1003.54 a	991.78	1028.50 a	10.38 b	24.96 a
Means	1.03 A	0.89 B	11.10 A	13.37 A	27.58 A	16.58 B	32.69 A	32.24 A	32.96 A	34.18 A	887.89 A	904.55 A	913.28 B	950.30 A	25.39 A	45.75 A
Shapiro-Wilks	ns		ns		ns		ns		ns		ns		ns		ns	
Thermal Env.	0.0217*		0.2731		0.0337*		0.8723		0.8083		0.2897		0.0085**		0.1473	
Genotype	<0.0001**		<0.0001**		<0.0001**		0.0234*		0.0026**		<0.0001**		<0.0001**		0.0155*	
Thermal Env.>block	0.4773		0.0004**		0.0355*		0.9082		0.6709		0.1939		0.5836		0.0324*	
Genotype* Thermal Env.	0.1526		0.0095**		0.3344		0.9107		0.8026		0.3684		0.3401		0.0330*	

Means, multiple comparisons test DGC, normality test and level of significance for treatment effect and their interaction. NSE: non-stress environment during critical period, SE: stress- environment during critical period. Means with the same lowercase letter are not significantly different ($p > 0.05$) within each thermal environment. Traits that are detailed with tiny letters only one thermal environment corresponds to the average of each genotype across environments. Means with the same capital letter are not significantly different ($p > 0.05$) between NSE and SE level

stress environment compared with non-stress environment

Eco-physiological components of grain yield

Heat stress around silking caused a severe Biomass_{pm} reduction (Table 5), in agreement with Rincón-Tuexi et al. (2006) and Mayer et al. (2012). Hybrids and inbred lines showed a Biomass_{pm} reduction under heat stress respect to non-stress environment from 2.07 to 1.77 kg m⁻² and from 1.03 to 0.89 kg m⁻², respectively. Hybrids HS8 and HS9 (both tropical) showed the highest Biomass_{pm}, whereas HS21 (temperate genotype) showed the lowest. Tropical genotypes HS7, HS9, HS11 HS12 and L3 showed the smallest variations of Biomass_{pm} across thermal environments. This Biomass_{pm} decrease is mainly explained by GY reduction, which could be a response of the modification of the plant's source capacity, being altered to a greater extent the temperate genetic background genotypes. Other works also reported the affection of the photosynthetic apparatus as one of the causes of the decrease in biomass (Wahid et al., 2007; Barnabás et al., 2008; Rattalino Edreira and Otegui, 2012; Ordoñez et al., 2015). In our study, the supra-optimal temperature at critical period for kernel set caused a decrease in the photosynthetic capacity of hybrids (decrease in CGR_{cp} from 28.49 gm⁻²d⁻¹ to 18.05 gm⁻²d⁻¹), however, in inbred lines this trait was not altered. In the inbred lines tested, even though CGR_{cp} was not modified across thermal environments, it could be observed the lowest CGR_{cp} under stress in temperate inbred lines (L5 and L6) and the highest CGR_{cp} in tropical inbred lines (L1 and L2). Heating around silking generated a lower photoassimilated production in plants during CP (lower CGR_{cp} in hybrids), moment in which there is a high demand for photoassimilates by the ear and other organs of the plant, so the kernel sink capacity could be reduced. Otherwise, certain tendency has been observed both in inbred lines and hybrids, that tropical genetic background presented greater source capacity than the temperate genetic background, as reported by Aluko and Fisher (1988) working on temperate and tropical single hybrids.

Heat stress around silking tended to decrease HI both in hybrids and inbred lines, with the exception of HS7, HS8, HS9, HS10, HS11, HS19 and L3, all with tropical genetic background (Table 5 and 6). The inbred lines showed HI decreases under stress, with the average of 27.58% and 16.58% in non-stress and heat stress environment, respectively. Hybrids showed GY decreases mainly through HI decreases due to heat stress, in agreement with previous evidences in maize (Rattalino Edreira and Otegui, 2012) and other crops (Ferris et al.,

1998; Craufurd et al., 2002).

Status indicators

It has been observed a decreasing tendency on SPAD_{postflag} value due to high temperatures, that decrease was statistically significant only in HS8, HS12, HS13, HS17 and HS19. In the same way, hybrids had altered SPAD_{postear} value across thermal environments, showing an average of SPAD_{postear} value of 46.71 and 41,62 in non-stress and heat stress environment, respectively, in agreement with Betran et al. (2003) working in maize under water stress. In inbred lines, no variation in leaf greenness was observed across thermal environments (Table 6), showing a tendency to present temperate genetic background inbred lines the lowest leaf greenness. The heat stress at CP damage generated in the photosynthetic apparatus of hybrids was captured by the post-stress leaf greenness decrease both in flag leaf and ear leaf, behavior not observed in inbred lines. According to Wahid et al. (2007) the photosynthetic apparatus is one of the components of the plants most sensitive to supra-optimal temperatures.

The study of the increase in leaf temperature as a consequence of a possible stomatal closure (Lösch, 1979) was used in numerous works under water stress in maize (Cárcova et al., 1998, Liu et al., 2011, Masuka et al., 2012), however, fewer studies were done under heat stress (Frey et al., 2015). In the present work, both hybrids and inbred lines showed no significant effect on any sources of variation for diftemp trait (data not shown).

The hybrid HS21 (temperate genetic background) showed the highest leaf rolling score, followed by HS13, HS14, HS15 and HS18, all of these hybrids under heat stress. The hybrids HS13, HS14, HS18, HS21 and L6 significantly increased their leaf rolling score under heat stress respect to non-stress environment (data not shown). The effect of high temperatures modified the leaf rolling in hybrids and inbred lines similar to that observed in other crops (Hasanuzzaman et al., 2013) however this depended on the genetic background of the plant. According to Wahid et al. (2007) plants tend to reduce heat-induced damage by leaf rolling, nevertheless, Lu et al. (2011) and Magorokosho et al. (2003), working on water stress, reported that leaf rolling can reduce the amount of light intercepted and grain yield. In the present work, it was possible to observe that hybrids with the greatest leaf rolling under heat stress had temperate or temperate x tropical genetic background. In general, under the same stress condition, temperate genetic background hybrids expressed early leaf rolling, while tropical hybrids did not yet show signs of stress. Therefore, leaf rolling could be consi-

dered as a negative trait since it could express a poor ability of the plant to tolerate stress situations due to high temperatures.

Phenological traits

In hybrids, VT and R1 showed significant effect of interaction T x G (Table 5). Under heat stress, HS18 and HS21 showed the highest cumulative sum of thermal time to reach R1 and HS12 the lowest one. In most hybrids, high temperatures tended to increase the cumulative sum of thermal time to silking, being statistically significant only in HS18, HS19 and HS21. In general, the inbred lines increased their cumulative sum of thermal time to reach R1 under heat stress environment compared with non-stress environment (from 913.28 to 950.30 degree-days) (Table 6). Under heat stress the cumulative sum of thermal time was higher to reach silking than anthesis in agreement with other authors investigating heat stress (Yan and Hunt, 1999; Cicchino et al., 2010a), drought (Hall et al., 1981; Herro and Johnson, 1981; Bolaños and Edmeades, 1993a) and N deficiency (Uhart and Andrade, 1995; D'Andrea et al., 2006), however, the effect of heat stress on the ASI depended on the genetic background. In our research hybrids and inbred lines showed a significant effect of interaction T x G on ASI (Table 5 and 6). Under heat stress, HS21 showed the highest ASI and HS8, HS9, HS11, HS12, HS13, HS14, HS15, HS16 and HS20 showed the lowest. The HS19, HS21 and L5 increased ASI when plants were subjected to heat stress around silking, in agreement with Cicchino et al., (2010b) and Zaidi et al., (2016) however disagreeing with Rattalino Edreira et al. (2011). A reduced ASI is a sign of a greater partition of the assimilated towards the ears around silking, allowing the stress tolerant genotypes to reach R1 earlier and have a higher ears biomass at anthesis (Cárcova and Otegui, 2001). In spite of the increase of R1 due to heat stress effect, in general, inbred lines and hybrids did not modify (data not shown) their cumulative sum of thermal time to reach physiological maturity (with the exception of HS11 and HS17), which could mean a shortening of the effective grain filling period of the genotypes in a heat stress environment.

Heat stress susceptibility and phenotypic plasticity

There was a positive relationship between grain yield in non-stress environment and grain yield in heat stress environment in hybrids ($r = 0.59$, $n = 45$, $p < 0.0001$) and inbred lines ($r = 0.66$, $n = 18$, $p < 0.0029$). On the other hand, there was a high negative correlation between HSI and grain yield under heat stress environment in hybrids ($r = -0.85$, $n = 45$, $p < 0.0001$) and inbred lines ($r = -0.80$, $n = 18$, $p < 0.0001$), meaning that more suscep-

tible genotypes to heat stress (genotypes with higher HSI) were in general those with lower GY under heat stress environment. Therefore, germplasm screening should be carried out under heat stress conditions and GY would be a key trait in selection process; however, considering other traits could increase the efficiency of selection of heat stress tolerant cultivars.

There was phenotypic variability of tolerance to heat stress across the maize inbred lines and hybrids evaluated. In the present work, it was possible to determine that tropical genotypes exhibited lower levels of kernel abortion and grain yield decreases than temperate genotypes under heat stress around CP. In other words, according to HSI values, HS13, HS14, HS15, HS16, HS18, HS19, HS20 and HS21 could be identified as heat-susceptible genotypes, the first seven temperate x tropical and the last one temperate genetic background (Table 1). The HS13 was the most heat-susceptible hybrid with GY decrease of 81.61% when subjected to heat stress. The HS9 and HS10 were tolerant to heat stress around CP, showing GY decreases of 23.11 and 12.57% under heat stress, respectively (Table 1); values that agree with those reported by Lobell et al. (2011). Even though HS8 has shown GY decreases of around 37% across environments, it was the second highest yielding under heat stress. In heat-tolerant hybrids, different strategies could be observed for maintaining GY across thermal environments. Heat-stress susceptible hybrids decreased KN, ED, CGR_cp, HI, SPAD_postflag, SPAD_postear and increased R1. The different strategies to produce grain yield indicate the presence of diverse packages of genes in each genotype to achieve the same goal. Such variability can be used in order to stack genes that meet these different strategies in a single genotype and thus achieve an improvement in behavior against heat stress. Regarding maize inbred lines, it was possible to characterize L5 as highly heat-susceptible, temperate genetic background genotype with GY decrease of 78% across thermal environments (Table 1). The L3 was the most heat-stress tolerant inbred line, tropical genetic background genotype with GY decreases lower than 1% (Table 1).

Some authors assessed the phenotypic plasticity in different crops (Sadras and Slafer, 2012; Peltonen-Sainio et al. 2011), in maize under different environmental index (Galizia et al. 2020) and different soil nutritional conditions (D'Andrea et al. 2013). To the best of our knowledge, this phenotypic plasticity has not been tested in maize under contrasting thermal environments. In the present work, we explored a wide range of phenotypic variation for GY and its yield components, both for maize hybrids and inbred lines. Regarding phenot-

ypic plasticity and considering all the data (through genotypes and thermal environments), we observed the greatest phenotypic plasticity (variation respect to the median greater than 50% in some of the distribution directions) for GY, KN, CGR_fill, HI and ASI (Fig. 2). On the contrary, traits, such as KW, Prol, ED, fPARI_cp, SPAD_postear, VT and R1 had the lowest plasticity (variation with respect to the median always lower than 25% in both directions of the distribution). Intermediate plasticity between the two extremes described above was found in Biomass_pm, SPAD_postflag and leaf rolling. In general, the 10th percentile represented the heat stress environment and the 90th percentile represented the non-stress environment, this occurred in traits, such as GY, KN, ED, EL, CGR_cp, CGR_fill, Biomass_pm and HI. This behavior was the opposite for traits, such as ASI, R1, VT and leaf rolling. Both groups of genotypes (hybrids and inbred lines) presented similar phenotypic plasticity in KW, ED, CGR_cp, VT, R1 and leaf rolling. The phenotypic plasticity for KN, Biomass_pm, CGR_fill and HI was always (in both thermal environments) higher in inbred lines than in hybrids (Fig.2). This similarity of the phenotypic plasticity pattern in inbred lines and hybrids indicates that most of the variation was due to the conditions imposed by the thermal environment and not due to the genotypes. No traits (except for the ASI in hybrids) had a plasticity greater than 2 (which is equivalent to a variation of 100% respect to the median), this agrees with Sadras and Slafer (2012) who reported a similar plasticity limit on the numerical components in small grain cereals and D'Andrea et al., (2013) working under contrasting soil nitrogen conditions. According to Westgate et al. (2004), a crop with poor tillering capacity and grain yield determined on a dominated axillary female inflorescence (such as maize) has reduced reproductive plasticity, compared with apical inflorescence crops (e.g. winter cereals) or crops with flowers distributed in most parts of the plant (for example, legumes) (Andrade, 1995). In the present work, this scarce variation in kernel number was confirmed under contrasting thermal environment, where it was restricted to 50% in hybrids and 60% in inbred lines. The plasticity of GY components under contrasting thermal environment decreased from those determined in initial stages to those determined later in the crop cycle (KN > KW), as documented for maize under different N conditions (D'Andrea et al., 2013) and other cereals (Sadras and Slafer, 2012). Phenological traits and most of the traits related to radiation use efficiency and the production of biomass had a low to intermediate plasticity. On the contrary, ASI and HI presented intermediate to high plasticities. It should be mentioned that traits with low plasticity would be good

predictors in the parental / progeny relationship. Therefore, since phenotypic plasticity is related to the predictive capacity of the lines in the formation of hybrids, this is promising for future heat-stress screening, in order to increase the selection efficiency in a breeding program. Nevertheless, based on these results, it could be interesting to advance with genetic analyzes that allow us to confirm our phenotypic analyzes.

Conclusions

Based on the evaluated traits, we were able to identify phenotypic variability of tolerance to heat stress during critical period for kernel set, both in hybrids and inbred lines. Heat stress during CP caused a GY decrease, however, it depended on the genetic background. Tropical genotypes exhibited lower levels of kernel abortion and grain yield decreases than temperate genotypes by heat stress effect. Heat-stress susceptible hybrids decreased KN, ED, CGR_cp, HI, SPAD_postflag, SPAD_postear and increased R1. Tropical genotypes HS8, HS9, HS10 and L3 could be identified as most tolerant to heat stress, while genotypes with a temperate x tropical and temperate genetic background HS13, HS14 and L5 were identified as most susceptible. It has been observed the greatest phenotypic plasticity for GY, KN, CGR_fill, HI and ASI. On the contrary, traits such as KW, Prol, ED, fPARI_cp, SPAD_postear, VT and R1 had the least plasticity. Germplasm screening should be carried out under heat stress conditions. Grain yield is a key trait in selection process, but considering other traits with low plasticity could increase the efficiency of selection of heat stress tolerant cultivars. This is promising for future heat-stress screening, in order to increase the selection efficiency in a breeding program.

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