

Cardinal temperatures of teocintle development (*Zea* spp.)

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Abstract

Teocintle represents an important source of genes for the improvement of maize (*Zea mays* L.); however, little progress has been made in the characterization of their responses to various environmental conditions, including the development of the teocintle as a function of temperature, this being a key variable for its adaptation and distribution. The base temperature (T_b), optimum temperature (T_o) and maximum threshold temperature (T_u) are also known as cardinal temperatures of development and are particular for each species, genotype and phenological stage. The objective of the present study was to determine the cardinal temperatures of the teocintle populations *Zea perennis*, *Zea diploperennis*, *Zea mays* subsp. *mexicana* races Chalco, Durango, Mesa Central and Nobogame and *Zea mays* subsp. *parviglumis* or race Balsas. Data from field experiments conducted between 1986 and 2005 were used where data from days to anthesis (F), temperature and precipitation data were monitored. Linear and curvilinear models were used to explain the variation of the development rate of the sowing-anthesis stage (1/F) as a function of the variation of the mean temperature (T_m) of the sowing-flowering period. The results showed that the relationship between T_m and 1/F is described by a curvilinear function, in all cases adjusting a quadratic-exponential model, with a value of $r^2 > 0.73$. The value of T_b varied from 8.02 to 14.31 °C, that of T_o between 23.5 and 31.67 °C and that of T_u between 29.43 and 40.61 °C. It is concluded that the cardinal temperature values of the teocintle vary between and within races, which indicates adaptation to various thermal conditions for the teocintle breeds studied.

Keywords: cardinal temperatures, maize genetic resources, populations of teocinte, wild relatives.

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Introduction

The teocintle represents an important source of genes for the improvement of maize (*Zea mays* L.) in aspects of nutritional quality, resistance to diseases, adaptation to abiotic stress conditions and agronomic quality (Cohen and Galinat 1984; Mano and Omori 2007; Wang *et al.*, 2008; Flint-García *et al.*, 2009). Hybridization with maize has been documented in all breeds and teocintle species in Mexico and Guatemala (Wilkes, 1967) spontaneous hybrids have occurred between maize and teocintle, which has allowed the transfer of genes between them (Ellstrand *et al.*, 2007).

The teocintle is represented by annual and perennial species, diploids and tetraploids, which are found in tropical and subtropical areas of Mexico, Guatemala, Honduras, Nicaragua, El Salvador and Costa Rica (Reeves, 1950; Sánchez *et al.*, 2011; Sánchez *et al.*, 2018). Teocintle populations do not have a uniform geographic distribution and the place of distribution is closely related to climate, soil and anthropogenic activities (Sánchez *et al.*, 2011). It adapts to different elevations (Wilkes, 1967; Ruiz *et al.*, 2001), which has led to its development taking place under different conditions of temperature, light and humidity. Wild populations of teocintle have coexisted for millennia with particular climatic conditions, which have probably led to different types of response to climate elements such as temperature and photoperiod.

This condition suggests the possibility of having teocintle with different levels of tolerance to different types of abiotic stress, such as tolerance to high and low temperatures. In this sense, the values of cardinal temperatures can constitute appropriate indicators of said tolerance, that is that a high maximum threshold temperature or a low minimum threshold temperature could be indicating a tolerant plant at high temperatures in the first case and at low temperatures in the second case.

However, the importance of teocintle as a wild relative and genetic resource for maize, little progress has been made in the characterization of its responses to diverse environmental conditions. One of them is the temperature-development relationship, a relationship that is considered one of the most determining factors for the adaptation and distribution of species (Monteith, 1977; Valladares *et al.*, 2014). In the absence of sensitivity to photoperiod or vernalization, the rate of development of a plant is a positive linear function of temperature (T) in the interval between the base T (T_b) and the optimum T (T_o) (Ruiz *et al.*, 2002). The rate of development has a value 0 to T equal to or less than T_b, and a maximum value for T_o. Above the T_o, the rate of development decreases to a maximum T threshold (T_u). This corresponds to a sigmoidal relationship between T and the rate of crop development (Orchard, 1976; Ruiz *et al.*, 2002). However, for thermo-phenological field data there are two common cases: a) T data located within the suboptimal range; and b) T data including the optimal and suboptimal intervals (Ruiz *et al.*, 2002). Within the range of suboptimal T, the relation rate of development-temperature is described by the following expression (Monteith, 1977).

$$1/F = \beta_0 + \beta_1 T$$

Where: F is the time from the beginning to the end of the phenological period; T is the average temperature of the period; and β_0 and β_1 are parameters of a simple linear regression equation and are equivalent to genotypic constants. The value of T_b is obtained by means of the quotient $-\beta_0/\beta_1$ (Summerfield *et al.*, Cited by Ruiz *et al.*, 2002).

For experimental data that include optimal and suboptimal temperatures and describe approximately a non-linear cloud of points, the determination of threshold temperatures should be done with a curvilinear model. The T_b (minimum threshold), T_o and T_u (maximum threshold) are also known as cardinal temperatures of development and are specific for each species, genotype and phenological stage (Del Pozo *et al.*, 1987; Derieux and Bonhomme, 1990; Duran *et al.*, 2011). Robertson (1983) suggests that the development-temperature relationship be described with a quadratic function if one wants to determine the value of T_b and T_o , or a quadratic-exponential function if the three cardinal temperatures are to be determined.

The objective of the present study was to determine the cardinal temperatures of the teocintle races *Zea perennis*, *Zea diploperennis*, *Zea mays* subsp. *mexicana* Chalco, Durango, Mesa Central and Nobogame and *Zea mays* subsp. *parviglumis* or Race Balsas.

Materials and methods

Teocintle populations

To take into consideration the influence of the genotype-environment interaction on the possible variation of the values of the cardinal temperatures, the phenological information and the determination of the values of the cardinal temperatures was organized taking as a unit of study the populations of teocintle within each race or subspecies. Next, each of the populations studied is described using the term geographic region.

Zea mays subsp. *parviglumis* (Race Balsas)

Region 1: includes the localities of Zacatongo, in the municipality of Mascota, Jal.; The Tablillo, located at km 10 Guachinango-The Cienega highway and km 10 Tepuzhuacan-Zacatongo highway, both belonging to the municipality of Guachinango, Jalisco. In the state of Nayarit includes the town of Amatlan of Cañas in the municipality of the same name. The latitudinal range of this teocintle population ranges from 20.62861 to 20.85556° north, while the longitudinal range ranges from 104.40833 to 104.54861° west, with an altitudinal range of 620 to 1 400 m.

Region 2: it is located in the state of Guerrero and includes the localities of Acahuizotla and Rincón of the Vía (km 45, highway 95), in the municipality of Mochitlan and the town of Palo Alto in the municipality of Chilpancingo of the Bravos. The latitudinal range of this teocintle population ranges from 17.28667 to 17.39806° north, while the longitudinal range ranges from 99.47306 to 99.4783° west, with an altitudinal range of 827 to 1 260 m.

Region 3: it is also located in the state of Guerrero and includes the localities of Ahuacatitlan (km 1.5 of the junction), Rincón of Sauce and Alcholoa (km 11 Teloloapan-Arcelia highway) in the municipality of Teloloapan. It also includes the town of Ixcateopan (The Tranca) located in the municipality of the same name. The latitudinal range of this teocintle population ranges from 18.33 to 17.41778° north, while the longitudinal range ranges from 99.40778 to 99.92139° west, with an altitudinal range of 1 450 to 1 920 m.

Region 4: it is located in the town of The Coyotomate, municipality of Ejutla, in the state of Jalisco. The latitudinal range of this teocintle population ranges from 19.9675 to 19.97333° north, while the longitudinal range ranges from 104.06861 to 104.58417° west, with an altitudinal range of 950 to 1 300 m.

Region 5: is located in the state of Mexico and includes the towns of The Puente (km 22 Luvianos-Zacazonapan highway, The Puerto (km 18 Luvianos-Zacazonapan highway) and the site located at km 2 Zacazonapan-Otzoloapan highway, municipality of Zacazonapan also includes the town of Sifon Colorines in the municipality of Valle of Bravo. The latitudinal range of this teocintle population ranges from 19.03889 to 19.18028° north, while the longitudinal range ranges from 100.22917 to 100.29258° west, with an altitudinal range from 1 085 to 1 468 m.

Region 6: is located in the state of Jalisco and includes the towns of The Lima and The Rodeo, municipality of Toliman. The latitudinal range of this teocintle population ranges from 19.52417 to 19.52833° north, while the longitudinal range ranges from 104.06139 to 104.06389° west, with an altitudinal range of 1 450 to 1 460 m.

Region 7: it is located in the state of Mexico in the Ruins of Malinalco at a latitude of 18.95333° north, longitude of 99.50278° west, and altitude of 1 850 m.

Region 8: it is located in the town of Queretanillo (km 24 Huetamo-Morelia highway), municipality of Tzitzio, in the state of Michoacan. The latitudinal range of this teocintle population ranges from 19.55056 to 19.58333° north, while the longitudinal range ranges from 100.91667 to 100.91806° west, with an altitudinal range of 1 342 to 1 500 m.

***Zea mays* subsp. *mexicana* (Race Chalco)**

Region 1: it is located in San Antonio Soyatzingo, municipality of Amecameca and in Temamatla, both in the State of Mexico. The latitudinal range of this teocintle population ranges from 19.08167 to 19.28194° north, while the longitudinal range ranges from 98.87167 to 98.88167° west, with an altitudinal range of 2 200 to 2 480 m.

Region 2: it is located mainly in the municipality of Chalco and in part of the municipality of Temamatla, State of Mexico. The latitudinal range of this teocintle population ranges from 19.18806 to 19.28194° north, while the longitudinal range ranges from 98.87167 to 98.88167° west, with an altitudinal range of 2 200 to 2 480 m.

***Zea mays* subsp. *mexicana* (Race Durango)**

Region 1: located in the towns of Francisco Villa (km 3) and Puente Dalila (km 7), highway 45 to Zacatecas, in the state of Durango. The latitudinal range of this teocintle population ranges from 24.01917 to 24.08528° north, while the longitudinal range ranges from 104.48583 to 104. 56056° west, with an altitudinal range of 2 200 to 2 480 m.

***Zea mays* subsp. *mexicana* (Race Mesa Central)**

Region 1: located in San Jeronimo (km 4 N), municipality of Ayotlan in the state of Jalisco, at a latitude of 20.41389 to 20.42056° north, a longitude of 102.34667° west and an altitude of 1 550 to 1 600 m.

Region 2: it is located in Cojumatlan of Regules (km 5.7 SW) in the state of Michoacán, at a latitude of 20.11389° north, longitude 102.89583° west and an altitude of 1 700 m.

Region 3: this teocintle population is distributed in the states of Michoacan and Guanajuato. In Michoacan, it is located in the San Agustin of Maiz, municipality of Copandaro; (km 2 south of Cuamio) municipality of Cuitzeo, km 267.5 highway Guadalajara-Morelia, municipality of Chucandiro; Hacienda The Estancia and at km 0.5 south of The Estancia, municipality of Huandacareo. In Guanajuato, it is located in the town of Uriangato. The latitudinal range of this teocintle population ranges from 19.87306 to 20.17° north, while the longitudinal range ranges from 101.15611 to 101.38694° west, with an altitudinal range of 1 785 to 2 019 m.

Region 4: corresponds to the teocintle of the locality of The Salitre in the municipality of Ixtlan, state of Michoacan, at 20.15333-20.15361° north latitude, 102.36417° west longitude and 1 530-1 574 m.

Region 5: it is located in the location of City Manuel Doblado in the state of Guanajuato, at 20.7225° north, 101.94194° west and 1 710 meters above sea level.

Region 6: includes the following sites: Batuecas (km 1.0 towards Cuitzeo), km 2 Puruandiro-Cuitzeo highway, km 3 Puruandiro-The Pilas highway, km 2 Puruandiro-Tortugas highway, km 6 Puruandiro-Villachuato highway, Puruandiro municipality, state from Michoacan.

Region 7: is located in the state of Michoacán and includes the towns of Jalapa (km 0.5 SW Jalapa) and km 1 Zinaparo-Churintzio highway, in the municipality of Zinaparo. In addition, in the municipality of Churintzio includes the Hill Churintzio, Changitiro (km 1 road to Purepero), the site located at km 334.5 of the Morelia-Guadalajara highway, the site at km 0.5 north of Churintzio, and the site located at km 3.2 of the Churintzio-The Noria road. Latitudinally it goes from 20.16944 to 20.17806° north latitude and longitudinally it goes from 102.00972 to 102.10694° west longitude, with an altitudinal interval of 1 801 to 1 940 m.

***Zea mays* subsp. *mexicana* (Race Nobogame)**

Region 1: this teocintle population is distributed in the vicinity of the Tarahumares stream, and in the transect between the Tejamanil-The Rinconada populations, in the municipality of Guadalupe and Calvo, in the state of Chihuahua. It is located at 26.21694-26.22389° north latitude, 104.58417-106.9625° west, with an altitudinal range of 1 919 to 1 950 m.

Zea diploperennis

Region 1: it is distributed in the towns of Manantlan, The Joyas and Corralitos in the municipality of Cuautitlan, Jalisco, with a latitudinal range of 19.59056 to 19.61667° north, a longitudinal range of 104.1159 to 104.30778° west and an altitude of 1 854 a 1 870 m

Zea perennis

Region 1: it is distributed in the localities of La Tinaja and Piedra Ancha, municipality of San Gabriel, and The Mesa, municipality of Zapotlan The Grande, in the state of Jalisco. It is located at 19.635-19.64333° north latitude, 103.56667-103.57722° west longitude and at 2 100-2 130 m.

Data of phenology and temperature

Data from field experiments conducted between 1986 and 2005 were used where data from days to flowering (F) and temperature (T) were recorded. In Table 1 you can see the description of the study environments. The sowing seed was obtained from the Maize Germplasm Bank of the INIFAP and the Postgraduate College, of which 105 accessions were sown during 1986, 110 during 1988 and 52 in 1991. Each accession was planted in a 10 m furrow with 25 plants each, under an experimental design of randomized complete blocks with three repetitions.

Table 1. Phenological observation environments.

Location	Year	Date of planting	Latitude (N)	Longitude (W)	Altitude (m)	Average temperature June-October (°C)
Chapingo, México	1986	June 22	19° 29'26	98° 53'06	2 250	17.69
Iguala, Guerrero	1986	June 22	18° 19'06	99°32'54	767	25.91
The Agujas, Jalisco	2003	June 24	20° 44'45	103°30'47	1 660	20.87
	2004	June 22	20° 44'45	103°30'47	1 660	21
	2005	June 27	20° 44'45	103°30'47	1 660	22
Tepatitlan, Jalisco	1986	June 22	20° 48'35	102°45'54	1 800	19.56
Tlajomulco, Jalisco	1991	June 22	20° 28'25	103°26'52	1 589	20.01
Zapopan, Jalisco	1988	June 22	20°41'40	103°23'41	1 579	21.97

Analysis procedure

For the flowering periods, in the seven observation environments, development rates were obtained by calculating 1/F. These values were plotted as a function of temperature to describe the trend of the data. Since the data described a curvilinear shape, it was decided to use the quadratic regression model (Robertson, 1983) to calculate the base temperature and the optimal temperature:

$$1/F = \beta_0 + \beta_1 T_m + \beta_2 T_m^2$$

Where: T_m is the average temperature of F. From this equation the base temperature was estimated as expressed in the following expression:

$$T_b = \frac{-\beta_1 \pm \sqrt{\beta_1^2 - 4\beta_0\beta_2}}{2\beta_2}$$

Where: T_b = base temperature; and the optimum temperature was calculated with the equation:

$$T_o = \frac{-\beta_1}{2\beta_2}$$

Once calculated T_b and T_o , the maximum threshold temperature was determined with the equation:

$$T_u = \frac{\ln(2C^{T_o} - C^{T_b})}{\ln C}$$

Where: \ln is the natural logarithm; and C equals 1.039. This value was obtained with a procedure of successive approximations.

Results and discussion

Figure 1 shows the observed relationship between temperature and the rate of development for the teocintles of the geographical type regions. As can be seen in the graphs of this figure, these two variables describe a curvilinear relationship, so it was possible to estimate the values of the cardinal temperatures, using the proposed methodology. However, as can be noted, the range of temperatures under which teocintle development was observed was relatively small. However, the range of temperatures explored with the field experiments covered almost all cases, thermal levels contained in the suboptimal and optimum intervals for the development of the teocintle. Only the cases of paragraphs a, d, f and p of Figure 1 show a curve without the thermal optimum plateau, so in the future additional phenological observations should be sought to generate better models. The quadratic regression model adequately represented in all cases the temperature-rate of development relationship. Due to the type of curve adjusted, it was possible to graphically identify the base temperature and the optimum temperature; not so the T_u , so it was necessary to use an exponential adjustment.

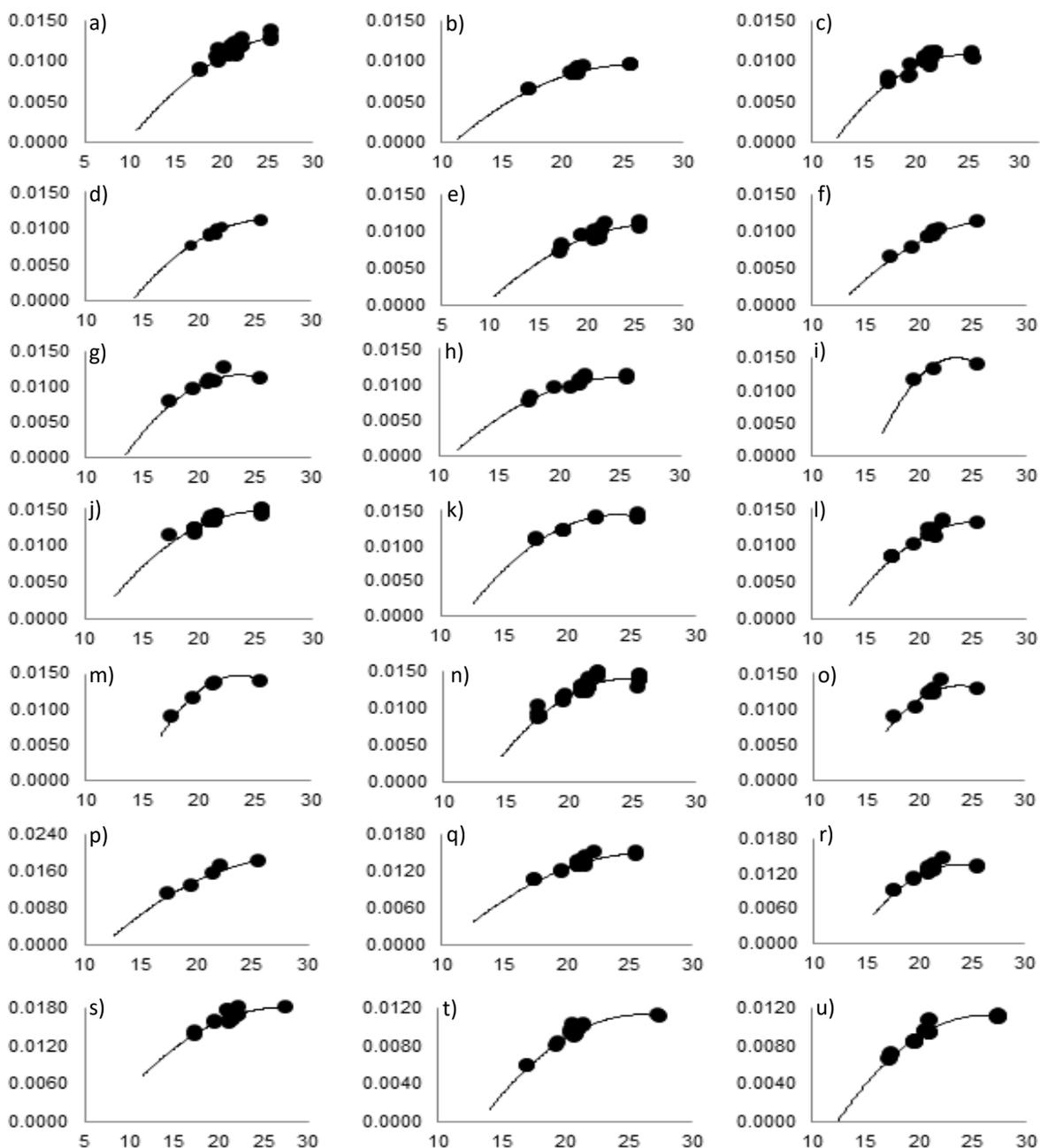


Figure 1. Relationship between temperature (X axis) and development rate (Y axis) in teocintle: a) Balsas Guachinango; b) Balsas Chilpancingo; c) Balsas Teloloapan; d) Balsas Ejutla; e) Balsas Zacazonapan; f) Balsas Toliman; g) Balsas Malinalco; h) Balsas Tzitzio; i) Chalco Amecameca; j) Chalco Chalco; k) Durango; l) Mesa Central Ayotlan; m) Mesa Central Cojumatlán; n) Mesa Central Chucandiro-Cuitzeo; o) Mesa Central Ixtlan; p) Mesa Central Manuel Doblado; q) Mesa Central Puruandiro; r) Mesa Central Churintzio; s) Nobogame; t) *Zea diploperennis*; and u) *Zea perennis*.

In Table 2, the values of the parameters of the quadratic regression and the cardinal temperatures obtained through the generated models are shown.

Table 2. Regression parameters and cardinal temperature values for teocintle.

Race/región	Región	β_0	β_1	β_2	T_b	T_o	T_u	R^2	T_u-T_b
Balsas (subsp. <i>parviglumis</i>)									
Guachinango	1	-0.0177	0.0022	-0.00004	9.79	27.5	35.83	0.84	26.04
Chilpancingo	2	-0.0193	0.0022	-0.00004	11	27.5	34.66	0.94	23.66
Teloloapan	3	-0.0316	0.0035	-0.00007	11.82	25	31.29	0.82	19.47
Ejutla	4	-0.0423	0.0041	-0.00008	14.31	25.62	29.43	0.93	15.12
Zacazonapan	5	-0.0149	0.0019	-0.00003	9.17	31.67	40.61	0.8	31.44
Tolimán	6	-0.0266	0.0027	-0.00005	12.96	27	32.15	0.98	19.19
Malinalco	7	-0.0501	0.0052	-0.0001	12.77	26	31.34	0.86	18.57
Tzitzio	8	-0.0236	0.0028	-0.00005	10.33	28	35.78	0.91	25.45
Chalco (subsp. <i>mexicana</i>)									
Amecameca	1	-0.0312	0.0036	-0.00007	11.03	25.71	32.79	0.79	21.76
Chalco	2	-0.0256	0.0031	-0.00006	10.31	25.83	33.63	0.82	23.32
Durango (subsp. <i>mexicana</i>)	1	-0.0419	0.0047	-0.0001	11.95	23.5	31.69	0.81	19.74
Mesa Central (subsp. <i>mexicana</i>)									
Ayotlán	1	-0.0388	0.0041	-0.00008	12.52	25.62	31.22	0.93	18.7
Cojumatlán	2	-0.1056	0.0103	-0.0002	14.13	25.75	29.74	0.93	15.61
Chucándiro-Cuitzeo	3	-0.0518	0.0054	-0.0001	12.47	27	32.64	0.86	20.17
Ixtlán	4	-0.0603	0.0062	-0.0001	12.08	31	37.04	0.85	24.96
M. Doblado	5	-0.0337	0.0036	-0.00006	11.6	30	36.51	0.96	24.91
Puruándiro	6	-0.0254	0.003	-0.00006	10.8	25	32.32	0.87	21.52
Churintzio	7	-0.0584	0.006	-0.0001	12.22	30	35.89	0.89	23.67
Nobogame (subsp. <i>mexicana</i>)	1	-0.0194	0.0029	-0.00006	8.02	24.17	34.26	0.73	26.24
<i>Zea diploperennis</i>	1	-0.0358	0.0036	-0.00007	13.47	25.71	30.36	0.95	16.89
<i>Zea perennis</i>	1	-0.0296	0.0031	-0.00006	12.64	25.83	31.31	0.94	18.67

T_b= base temperature (°C); T_o: Optimum temperature (°C); T_u= maximum threshold temperature (° C). β_0 , β_1 ; β_2 = parameters of the quadratic regression.

The values of r^2 were located above 0.8, with the exception of two cases in which the value of this statistic was between 0.73 and 0.79. The minor adjustment in these models could be pointing to the influence of other factors on teocintle phenology, such as the photoperiod (Hung *et al.*, 2012) or soil moisture (Payero *et al.*, 2006), considering that the analyzed data they are from temporary crops.

Although it is proven that the photoperiod exerts an important influence on the duration of the teocintle development cycle, delaying flowering in long day environments (Hung *et al.*, 2012), in the field data analyzed and considering the adjustment from the obtained models, it can be said that the effect of the photoperiod variable remained constant in all the field studies used, since they all developed in the spring-summer cycle.

As can be seen in Table 2, both the base temperature and maximum temperature and optimum temperature values vary among the teocintle populations studied. This shows a capacity of variant thermal adaptation among the teocintle that inhabit different eco-geographic regions, which is a product of the plant-environment interaction experienced for centuries in these millenary plants (Wilkes, 1967). When comparing the values of T_b obtained for the teocintle with the values of T_b for the different races of maize (Ruiz *et al.*, 1998), it is possible to notice that the maize has achieved a greater adaptation to more temperate environments, given that the races Apachito, Cristalino of Chihuahua, Azul, Gordo, Palomero of Chihuahua, Palomero Toluqueño, Arrocillo, Conico, Elotes Conicos, Cacahuacintle, Chalqueño, Mushito, Serrano of Jalisco, Conico Norteño, Ancho, Bofo, Elotes Occidentales, Tablilla of Ocho, Zamorano Amarillo, Bolita, Jala, Comiteco, Coscomatepec, Oloton, Raton, Reventador, Onaveño y Dulcillo show a T_b lower than 8 °C.

In relation to corn, whose typical base temperature (10 °C) is widely cited (Gilmore and Rogers, 1958, Cross and Zuber, 1972, Neild, 1982, Cutforth and Shaykewich, 1989, Ruiz *et al.*, 2002), the teocintles with the greatest similarity presented (10 ± 1 °C) were Balsas Guachinango, Balsas Chilpancingo, Balsas Zacazonapan and Tzitzio Balsas, as well as Mesa Central Puruandiro and Chalco Amecameca, so these populations may have a thermal adaptation capacity similar to the original maize according to Matsuoka *et al.* (2002) was derived from *Zea mays ssp. parviglumis*.

The adaptation and development of plant species is conditioned by threshold temperatures of minimum and maximum development, also called physiological zeros. Below the minimum threshold and above the maximum threshold, cellular activity and therefore the development of the organism are considered null (Ruiz *et al.*, 2002). According to this, the teocintle that would have cell activity and therefore growth and development at the lowest temperatures would be the Nobogame teocintle, whose base temperature value is 8 °C (Table 2). While the teocintles that would have cellular and photosynthetic activity at the highest temperatures would be the Zacazonapan Balsas, Mesa Central Ixtlán, Mesa Central Manuel Doblado and Central Table Churintzio teocintle, with a T_u value of 40.61, 37.04, 36.51 and 35.89 °C, respectively (Picture 2). These same teocintles also stand out for having the highest optimum temperature value, above 30 °C. These populations of teocintle could indicate the presence of functional germplasm in warm environments, of high temperatures, which could represent an advantageous characteristic of teocintle, in addition to those already reported for teocintle, such as adaptation to drought (Sánchez *et al.*, 2018), flooded environments (Mano and Omori, 2015), resistance to diseases (Nault, 1983) and others. These populations could be a source of genes to incorporate tolerance to high temperatures in corn breeding programs.

Annual Mexican teocintles show genetic sub-structures along geographic lines (Fukunaga *et al.*, 2005), which establishes an interaction of the taxon with varying environmental conditions, and a selection pressure of plants (Coop *et al.*, 2010), ensuring that the diverse populations of these teocintle are adapted to certain particular conditions of temperature, precipitation (water) and solar radiation (basic environmental inputs for a plant). This may explain the intra- and inter-racial variability observed in the values of the cardinal temperatures studied. Some high values of T_b in Table 2 result with little correspondence with the geographical region of the population, such as the Teocintle Mesa Central Cojumatlan, with a T_b of 14.13 °C, in a geographical region at 1 700 m

altitude with a semi-warm climate and an average annual temperature around 19 °C. Given that the teocintle of this region must be acclimated to these environmental conditions, it is advisable to take this T_b value with reservations and to try in the near future to do a re-analysis including more phenology data of this population.

Conclusions

There are intra- and inter-racial differences in relation to the values of the cardinal temperatures of the various populations of teocintle, which indicates that the teocintle has an adaptation to different temperature conditions through the types of teocintle known.

The cardinal temperature values obtained allow us to conclude that considering the different populations of teocintle, the physiological zeros (threshold temperatures) go beyond the thermal range of a typical corn ($T_b= 10\text{ °C}$; $T_u= 30\text{ °C}$), so there is an interesting potential for incorporating teocintle threshold temperatures into maize, especially considering improving the adaptation of this crop to the increasingly warmer production environments that climate change is bringing.

It is desirable in the future to incorporate more data of phenology and temperature to the analysis of cardinal temperatures of some of the studied populations to obtain more robust results in relation to the determination of the values of the cardinal temperatures of teocintle. However, the results of the present study can be considered as a valuable first quantitative report about the issue of cardinal temperatures of teocintle.

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Cited literature

- Cohen, J. I. and Galinat, W. C. 1984. Potential use of alien germplasm for maize improvement. *Crop. Sci.* 24(6):1011-1015.
- Coop, G.; Witonsky, D.; Di Rienzo, A. and Pritchard, J. K. 2010. Using environmental correlations to identify loci underlying local adaptation. *Genetics.* 185(4):1411-1423.
- Cross, H. Z. and Zuber, M. S. 1972. Prediction of flowering dates in maize based on different methods of estimating thermal units. *Agron. J.* 64(3):351-355.
- Cutforth, H. W. and Shaykewich, C. F. 1989. Relationship of development rates of corn from planting to silking to air and soil temperature and to accumulated thermal units in a prairie environment. *Can. J. Plant Sci.* 69(1):121-132.
- Del Pozo, A. H.; García, H. J.; Novoa, R. and Villaseca, S. 1987. Relationship of base temperature to development of spring wheat. *Exp. Agric.* 23(1):21-30.

- Derieux, M. and Bonhomme, R. 1990. Heat units requirements of maize inbred lines for pollen shedding and silking: Results of the European FAO Network. *Maydica*. 35(1):41-46.
- Durán, P. N.; Ruiz, J. A.; González, E. C. D. R.; Núñez, H. G.; Padilla, R. F. J. y Contreras R. S. H. 2011. Temperaturas cardinales de desarrollo en la etapa siembra-emergencia de 11 pastos forrajeros. *Rev. Mex. Cienc. Pecu.* 2(3):347-357.
- Ellstrand, N. C.; Garner, L. C.; Hegde, S.; Guadagnuolo, R. and Blancas, L. 2007. Spontaneous hybridization between maize and teosinte. *J. Heredity*. 98(2):183-187.
- Flint, G. S. A.; Bodnar, A. L. and Scott, M. P. 2009. Wide variability in kernel composition, seed characteristics, and zein profiles among diverse maize inbreds, landraces, and teosinte. *Theor. Appl. Genet.* 119(6):1129-1142.
- Fukunaga, K.; Hill, J.; Vigouroux, Y.; Matsuoka, Y.; Sánchez, G. J. J.; Liu, K.; Buckler, E. S. and Doebley, J. 2005. Genetic diversity and population structure of teosinte. *Genetics*. 169(4):2241-2254.
- Gilmore, E. and Rogers, J. S. 1958. Heat units as a method of measuring maturity in corn. *Agron. J.* 50(10):611-615.
- Hung, H. Y.; Shannon, L. M.; Tian, F.; Bradbury, P. J.; Chen, C.; Flint, G. S. A.; McMullen, M. D.; Ware, D.; Buckler, E. S.; Doebley, J. F. and Holland, J. B. 2012. ZmCCT and the genetic basis of day-length adaptation underlying the postdomestication spread of maize. *PNAS*, E1913-E1921. doi/10.1073/pnas.1203189109.
- Mano, Y. and Omori, F. 2007. Breeding for flooding tolerant maize using “teosinte” as a germplasm resource. *Plant Root*. doi:10.3117/plantroot.1.17.1:17-21.
- Mano, Y. and Omori, F. 2015. Flooding tolerance in maize (*Zea mays* subsp. *mays*) F1 hybrids containing a QTL introgressed from teosinte (*Zea nicaraguensis*). *Euphytica*. 205(1):255-267.
- Matsuoka, Y.; Vigouroux, Y.; Goodman, M. M.; Sánchez, G. J. J.; Buckler, E. and Doebley, J. 2002. A single domestication for maize shown by multilocus microsatellite genotyping. *PNAS*. 99(9):6080-6084.
- Monteith, J. L. 1977. Climate. *In: ecophysiology of tropical crops*. Alvim, T. and Kozlowski, T. T. (Eds.). Academic Press. New York. 1-25 pp.
- Nault, L. R. 1983. Origins of leafhopper vectors of maize pathogens in Mesoamerica. *In: Gordon, D. T. Knoke, J. K.; Nault, L. R. and Ritter, R. M. (Eds.). Proceedings international maize virus disease colloquium and workshop. 2-6 August 1982. The Ohio State University, Ohio Agricultural Research and Development Center, Wooster. USA. 75-82. pp.*
- Neild, R. E. 1982. Temperature and rainfall influences on the phenology and yield of grain sorghum and maize: a comparison. *Agric. Meteorol.* 27(1-2):79-88.
- Orchard, T. J. 1976. The constant temperature equivalent. *Scientia Hort.* 4(4):299-307.
- Payero, J. O.; Melvin, S. R.; Irmak, S. and Tarkalson, D. 2006. Yield response of corn to deficit irrigation in a semiarid climate. *Agric. Water Manag.* 84(1-2):101-112.
- Reeves, R. G. 1950. The use of teosinte in the improvement of corn inbreds. *Agron. J.* 42(7):248-251.
- Robertson, G. W. 1983. Weather-based mathematical models for estimating development and ripening of crops. Technical Note No. 180. WMO No. 620. Geneva, Switzerland. 99 p.
- Ruiz, C. J. A.; Sánchez, G. J. J. and Goodman, M. M. 1998. Base temperature and heat unit requirement of 49 mexican maize races. *Maydica*. 43(4):277-282.
- Ruiz, C. J. A.; Sánchez, G. J. J. and Aguilar, S. M. 2001. Potential geographical distribution of teosinte in Mexico: A GIS approach. *Maydica*. 46(2):105-110.

- Ruiz, C. J. A.; Flores, L. H. E.; Ramírez, D. J. L. y González, E. D. R. 2002. Temperaturas cardinales y duración del ciclo de madurez del híbrido de maíz H-311 en condiciones de temporal. *Agrociencia*. 36(5):569-577.
- Sánchez, G.; De La Cruz, L.; Vidal, M.; Ron, P.; Taba, S.; Santacruz, R. F.; Sood, S.; Holland, B.; Ruiz, J.; Carvajal, S.; Aragón, C.; Chávez, T.; Morales, R. and Barba, G. R. 2011. Three new teosintes (*Zea* spp., *Poaceae*) from México. *Am. J. Bot.* 98(9):1537-1548. DOI: 10.3732/ajb.1100193.
- Sánchez, G. J. J.; Ruiz, C. J. A.; Medina, G. G.; Ramírez, O. G.; De la Cruz, L. L.; Holland, J. B.; Miranda, M. R. and García, R. G. E. 2018. Ecogeography of teosinte. *PLoS ONE*. 13(2):e0192676. <https://doi.org/10.1371/journal.pone.0192676>.
- Valladares, F.; Matesanz, S.; Guilhaumon, F.; Araújo, M.B.; Balaguer, L.; Benito, G. M.; Cornwell, W.; Gianoli, E.; van Kleunen, M.; Naya, D. E.; Nicotra, A. B.; Poorter, H. and Zavala, M. A. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*. 17(11):1351-1364.
- Wang, L.; Xu, C.; Qu, M. and Zhang, J. 2008. Kernel amino acid composition and protein content of introgression lines from *Zea mays* ssp. *mexicana* into cultivated maize. *J. Cereal Sci.* 48(2):387-393.
- Wilkes, H. G. 1967. Teosinte: the closest relative of maize. Cambridge, Massachusetts: The Bussey Institute. Harvard University. 159 p.