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Ecology

Are the *Dioon edule* (Zamiaceae) forms from San Luis Potosí proposed by Whitelock (2004) recognizable? Morphological evidence

¿Son reconocibles las formas de Dioon edule *(Zamiaceae) de San Luis Potosí propuestas por Whitelock (2004)? Evidencia morfológica*

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Abstract

Based on their morphological traits and elevation distribution, we analyzed 15 populations of *Dioon edule* and *D. angustifolium* located in the Sierra Madre Oriental in an elevation gradient from 294 to 1,314 m asl, to identify the forms proposed by Whitelock (2004). A non-parametric test was applied to find differences among elevation and populations. A discriminant analysis was applied to classify the population forms and calculate the proportion of well-classified observations, as well as Maxent to select the environmental predictors of the population's distribution. Ten populations were grouped into 3 forms proposed by Whitelock (2004): "angustifolium", "edule" and "rioverde", but 5 populations could not be classified as proposed forms, and they were named "tamasopo". The forms "tamasopo" and "rioverde" present intermediate values between the 2 species, with 63% of the individuals classified as "tamasopo" and 25% as "rioverde". Individuals with greater height, diameter, leave length and leave number correspond to the "edule" form in the lowest elevation. The most important variables to define the distribution of the populations are vegetation, slope and annual precipitation.

Keywords: Classification; *Dioon edule*; Elevation; Environmental variables; Morphological traits

Resumen

En función de sus rasgos morfológicos y distribución de elevación, analizamos 15 poblaciones de *Dioon edule* y *D. angustifolium* ubicadas en la sierra Madre Oriental en un gradiente de elevación de 294 a 1,314 m snm, para identificar las formas propuestas por Whitelock (2004). Se aplicó una prueba no paramétrica para encontrar diferencias

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entre la elevación y las poblaciones. Se aplicó un análisis discriminante para clasificar las formas de las poblaciones y calcular la proporción de observaciones bien clasificadas, así como a Maxent para seleccionar los predictores ambientales de la distribución de las poblaciones. Diez poblaciones se agruparon en 3 formas propuestas por Whitelock (2004): "angustifolium", "edule" y "rioverde", pero 5 poblaciones no pudieron clasificarse como formas propuestas y se llamaron "tamasopo". Las formas "tamasopo" y "rioverde" presentan valores intermedios entre las 2 especies, con 63% de los individuos clasificados como "tamasopo" y 25% como "rioverde". Los individuos con mayor altura, diámetro, longitud de hojas y número de hojas corresponden a la forma "edule" en la elevación más baja. Las variables más importantes para definir la distribución de las poblaciones son la vegetación, la pendiente y la precipitación anual.

Palabras clave: Classificación; *Dioon edule*; Elevación; Variables ambientales; Rasgos morfológicos

Introduction

Dioon edule Lindl. (Zamiaceae) is the species with the widest geographical range in Mexico from the genus *Dioon*. It is distributed along the Sierra Madre Oriental (SMO), from southern Tamaulipas throughout San Luis Potosí, Hidalgo, Querétaro, and Veracruz, with 1,525 m asl (de Luca et al., 1982; Whitelock, 2004; Yáñez-Espinosa, 2006). In the northernmost region of the Sierra Madre Oriental, in Tamaulipas and Nuevo León, there are small populations of *D. edule* var. *angustifolium*, disjunct and with restricted distribution areas (de Luca et al., 1982; González et al., 2008; Whitelock, 2004), recognized recently with the species status as *Dioon angustifolium* Miq. (González-Astorga et al., 2003). The populations of this species are confined to rocky canyons in transition zones between piedmont scrub and tropical dry forest or oak forest. The plants mainly develop in shallow soil (Lithosol), with a depth not exceeding 15 cm, clayey texture, pH of 7.54 and approximately 24% of organic matter (Chávez-Acuña, 2010; Rubio-Méndez, 2010). This species has played a relevant role in the indigenous cultures of the Sierra Madre Oriental. It has been used as a ceremonial, ornamental, medicinal, and food when maize is scarce (Bonta et al., 2019; Chávez-Acuña, 2010; Tristán-Martínez, 2012; Yáñez-Espinosa, 2006).

Due to the diversity of habitats in which *Dioon edule* grows and based on the observed morphological variation in populations (de Luca et al., 1982; Whitelock, 2004) along a latitudinal gradient in the Sierra Madre Oriental, from the northernmost distribution area in Nuevo León and Tamaulipas to central Veracruz (Table 1), some studies have recognized that there is intraspecific variation in some morphological traits, proposing the classification of *D. edule* populations in 7 "forms". However, these studies warned readers about not having included more populations distributed in the Sierra Madre Oriental (Whitelock, 2004). Particularly in the state of San Luis Potosí, Whitelock (2004) described the forms “ríoverde” and “valles”, which have been recognized in this study during the field trips carried out since 2008 to identify and characterize *Dioon edule* populations in the Sierra Madre Oriental of San Luis Potosí. However, there are more populations which show suggestive characteristics of other morphological forms not described by Whitelock (2004). Some studies also highlight the importance of comparing the phenotypic variation among *Dioon* species and their correlation to habitats to understand the evolutionary response to the environment, particularly to aridity (Gutiérrez-Ortega, Yamamoto et al., 2018).

Here, we analyze the main morphological traits of plants in the populations along the Sierra Madre Oriental

Table 1
Forms proposed by Whitelock (2004) to classify *Dioon edule* populations in its distribution area.

Form	Distribution area	Elevation (m asl)	Stem diameter (cm)	Height (cm)	Leaves No. per flush	Leaf length (cm)
“angustifolium”	Nuevo León, Tamaulipas	450-1075	17.5-22.5	100	-	80
“rioverde”	San Luis Potosí	430-740	22.5	150-180	-	120
“valles”	San Luis Potosí	150	-	30	3-4	55-75
“querétaro”	Querétaro	1230	-	120	-	70-100
“hidalgo”	Hidalgo	1385	22.5-25	300	-	120
“palma sola”	Veracruz	200	25	100 (300)	-	90-100
“edule”	Veracruz	150-300	25-30	100 (500)	-	80-130

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of *Dioon edule* in San Luis Potosí and Querétaro and of *D. angustifolium* in Nuevo León and Tamaulipas, to recognize and classify populations into the 2 forms proposed by Whitelock (2004) in the state of San Luis Potosí, as well as possible new ones. Also, we related them to environmental and geographic variables that could explain this phenotypic variation.

Materials and methods

This study was conducted in the Sierra Madre Oriental in Mexico, considering 3 populations of *D. angustifolium* in Nuevo León and Tamaulipas, and 12 populations of *Dioon edule* located in the states of San Luis Potosí and Querétaro. A latitudinal range from 24°51’ to 21°30’ N, and an elevation range from 294 to 1,314 m asl were covered (Fig. 1). The study was conducted in the summer of 2007 to 2018. The populations were classified in the forms proposed by Whitelock (2004) according to their elevation range (Table 1). In each population, 2 sites of 100 m^2 each were randomly selected and mature plants, defined as those in the reproductive stage of the life cycle with a visible stem and leaves arranged in 1 or more well-developed crowns, were evaluated. The parameters that were measured in each plant were plant total height, stem diameter, leaves number and leaf length.

A discriminant analysis (DA) was carried out to classify the 15 populations (n = 318) in the 3 forms defined by Whitelock (2004) for the Sierra Madre Oriental of San Luis Potosí, delimit the morphological traits of each form, and identify those that were not included in the range. A Kruskal-Wallis test was applied to assess for significant differences on elevation groups and populations for parameters because the measurement variables did not have a normal distribution not even with data transformation.

Populations were represented in Arcgis 10.3, to conduct a spatial analysis to identify the environmental features of the sites at which the populations grow. The environmental variables considered in the analysis were: annual mean temperature, and annual precipitation (1970-2010) obtained from the Worldclim database (Hijmans, 2012). The geographical layers were geology, edaphology, altitude, slope and the use of the soil and vegetation of the series V, generated from the digital elevation model of INEGI (2013). All layers were represented in raster format with a spatial resolution of 30 m. The maximum entropy of the Maxent 3.4.1 program algorithm was used to estimate the contributions of each variable, as well as their respective parameters. A Pearson correlation analysis among plant traits (leaf length and plant height), geography and environmental variables was performed to assess their association. All statistical analyses were performed with the software Xlstat v.2014.1.0.1 (Addinsoft, France).

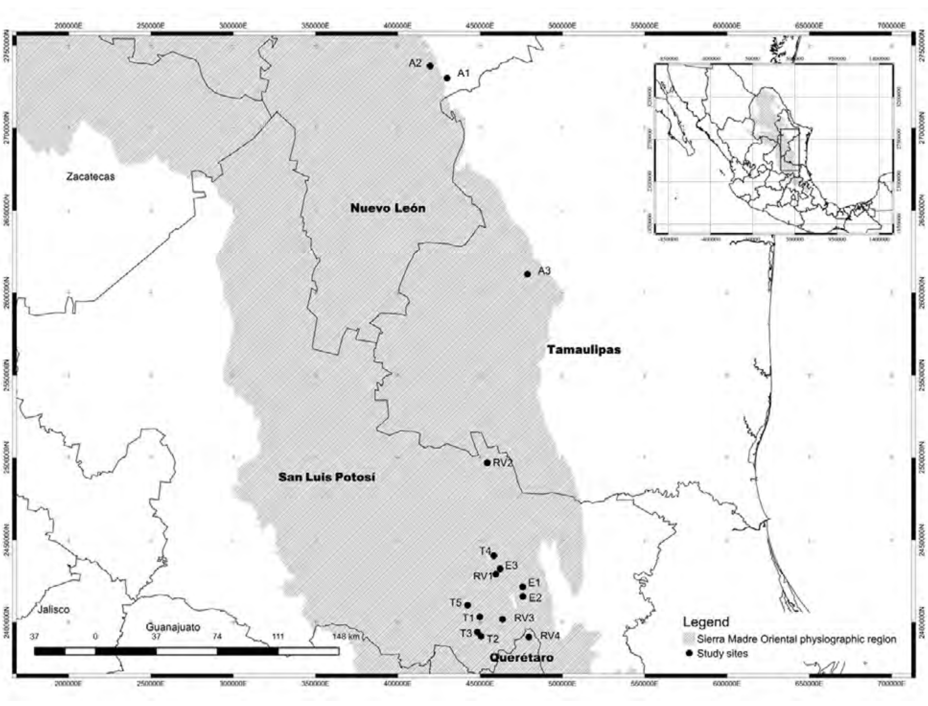

Figure 1. Study area in the Sierra Madre Oriental, México.

Results

The *Dioon edule* forms according to Whitelock (2004). The DA showed that the vectors of the 4 forms were significantly different ($p < 0.0001$). The populations were classified into 4 groups according to their morphological traits. Three of the forms corresponded to those proposed by Whitelock (2004): "edule" (3 populations), "rioverde" (4) and "angustifolium" (3). Five populations that were not classified because they did not fit the ranges established by Whitelock are now proposed to be a new form and designated "tamasopo" (Table 2, Fig. 2). It is remarkable that almost 40% of individuals of the "angustifolium" populations share morphological traits with the "tamasopo" form, but only 25% with the form "rioverde" and less than 4% with the "edule" form.

Two discriminant functions explained 99% of the total variability, contributing significantly to the separation between forms for the 15 populations ($p < 0.0001$, n = 313). The first function (eigenvalue = 0.311) explained 79.55% of the total variation, the second (eigenvalue = 0.076) explained 19.55%, and the third (eigenvalue = 0.004) explained the remaining variation. Morphological traits that contributed significantly to the separation of the centroids were leaf length, stem diameter and leaves number (Table 3).

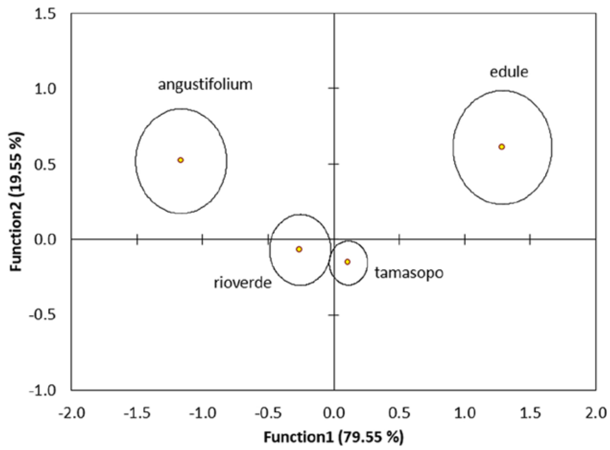

Figure 2. Discriminant Analysis biplot of the *Dioon edule* form "edule", "rioverde", "tamasopo" and *D. angustifolium* classification.

The species *Dioon edule* has the widest stem diameter and longer leaves than the other forms, while *D. angustifolium* presented the lowest values concerning stem diameter and leaf length. However, both species have the largest numbers of leaves, a trait which separates them from the other *D. edule* forms (Table

Table 2
Classification of *Dioon edule* and *D. angustifolium* populations based on their elevation range.

Species	Population	State	N	Elevation	Form
D. edule	E1	San Luis Potosí	7	294	"edule"
D. edule	E2	San Luis Potosí	4	314	"edule"
D. edule	E3	San Luis Potosí	16	384	"edule"
D. edule	RV1	San Luis Potosí	10	447	"rioverde"
D. edule	RV2	San Luis Potosí	12	600	"rioverde"
D. edule	RV3	San Luis Potosí	25	735	"rioverde"
D. edule	RV4	Querétaro	23	740	"rioverde"
D. edule	T1	San Luis Potosí	54	850	"tamasopo"
D. edule	T2	San Luis Potosí	25	862	"tamasopo"
D. edule	T3	San Luis Potosí	9	871	"tamasopo"
D. edule	T4	San Luis Potosí	6	931	"tamasopo"
D. edule	T5	San Luis Potosí	95	1,114	"tamasopo"
D. angustifolium	A1	Nuevo León	15	570	"angustifolium"
D. angustifolium	A2	Nuevo León	12	800	"angustifolium"
D. angustifolium	A3	Tamaulipas	5	1,314	"angustifolium"

4, Fig. 3). Significant statistical differences were found in all parameters measured by population pairs. As for the base diameter, the edule form is different from the "angustifolium" ($p < 0.005$), "rioverde" ($p < 0.0001$), and "tamasopo" ($p < 0.0001$) forms. The "tamasopo" form is, in turn, different from "angustifolium" ($p < 0.005$) and "rioverde" ($p < 0.005$). In height, "edule" was different from "angustifolium" ($p < 0.0001$) and "rioverde" ($p < 0.001$) and "tamasopo" was different from "angustifolium" ($p < 0.05$) and "rioverde" ($p < 0.05$). Regarding the leaves, there was only a difference between the "edule" and "tamasopo" forms ($p < 0.005$). In the leaf number per flush, "angustifolium" is different from "rioverde" ($p < 0.0001$) and "tamasopo" ($p < 0.0001$), while "edule" is different from "rioverde" ($p < 0.05$) and "tamasopo" ($p < 0.01$).

The "tamasopo" form occurs in several locations at an altitude of 850-1114 m asl (Fig. 3c). Stems are about 0.1-1 m in height and 0.02-0.3 m in diameter. The leaves are flat, about 1.34 m in length. Leaflets are straight, revolute, spiny, of 7.29 cm (± 0.11) in length and 0.56 cm (± 0.01) in width, inserted in acute angle in the yellowish rachis, with 0.25 cm (± 0.005) between them. Female cones are ovoid, densely tomentose, light brown, 205-260 mm long and 122-175 cm in diameter, male cones are cylindrical with conical apex, whitish green. Seeds are ovoid, the sarcotesta is light yellow to orange.

Table 3

Standardized coefficients of discriminant functions of *Dioon edule* and *D. angustifolium* populations. * Traits with a high contribution

Morphological traits	Standardized coefficients	
	Function 1	Function 2
Stem diameter	0.597*	0.216
Total height	0.274	-0.597
Leaves number	-0.274	0.968*
Leaf length	0.726*	0.07

In general, the largest diameter was found in population E2, as well as the largest number of leaves; on average, these were also the longest (Table 3). The tallest plants were found in T4 and the highest leaf production was found in E3 (Table 5). Significant differences were found in all parameters measured between population pairs (Table 6). For diameter, population T2 is different from RV4 ($p < 0.05$), RV2 ($p < 0.0001$), T5 ($p < 0.001$), A3 ($p < 0.05$) and T1 ($p < 0.0001$). In turn, T1 is different from T5 ($p < 0.05$) and E3 ($p < 0.0001$). This is different from RV2 ($p < 0.05$) and T5 ($p < 0.05$), which is also different from RV2 ($p < 0.05$) and A3 ($p < 0.05$).

For plant height, T5 was different from T1 ($p < 0.05$), RV2 ($p < 0.05$), and A3 ($p < 0.05$). T4 was different from T1 ($p < 0.01$) and A1 ($p < 0.05$), and T2 was different from A3 ($p < 0.05$). Regarding the number of leaves, T2 was different from A2 ($p < 0.05$), RV3 ($p < 0.01$) and E3 ($p < 0.05$). For leaves number per flush, T5 is different to A1 ($p < 0.001$) and E3 ($p < 0.01$). For leaf length, T5 is different from T2 ($p < 0.001$), RV4 ($p < 0.001$), A2 ($p < 0.01$), A3 ($p < 0.05$), A1 ($p < 0.05$) and T4 ($p < 0.05$). Population E3 is different from T2 ($p < 0.05$), RV4 ($p < 0.001$), A2 ($p < 0.001$) and A1 ($p < 0.005$), and population T4 is different from RV4 ($p < 0.005$) and A1 ($p < 0.05$).

Overall, 40% of the georeferenced sites are located at altitudes ranging from 497 to 925 m. In addition, 66% of field records indicate that the species develop on slopes lower than 14°, where soils tend to be deeper due to the accumulation of materials. Precipitation had the greatest contribution, followed by slope, vegetation, elevation and geology (Table 7). The remaining variables did not contribute to the model. The most relevant variables that

Table 4

Mean (±SE; range) morphological traits of the 4 forms of *Dioon edule* and *D. angustifolium* in their distribution range.

Form	Stem diameter (cm)	Total height (cm)	Leaves number	Leaves No. per flush	Leaf length (cm)
"angustifolium"	16.9 (±1.42; 0-34)	21.4 (±3.06; 0-55)	21.06 (±1.88; 1-52)	8.25 (0.69; 1-18)	62.82 (±4.82; 0-103)
"edule"	26.18 (±1.36; 17.5-45)	46.9 (±4.47; 20-13)	25.40 (±2.73; 8-65)	7.92 (1.34; 2-31)	105.951 (±4.21; 56-141.33)
"rioverde"	18.91 (±0.93; 5-63.3)	30.79 (2.5; 3-123)	19.05 (±1.34; 4-46)	5.51 (0.788; 1-49)	80.12 (±2.59; 41-121.75)
"tamasopo"	20.81 (±0.32; 11.04-33.74)	38.22 (±1.44; 0.775-100)	16.84 (±0.73; 0.88-44)	4.68 (0.46; 1-16)	82.75 (±3.36; 25.6-134)

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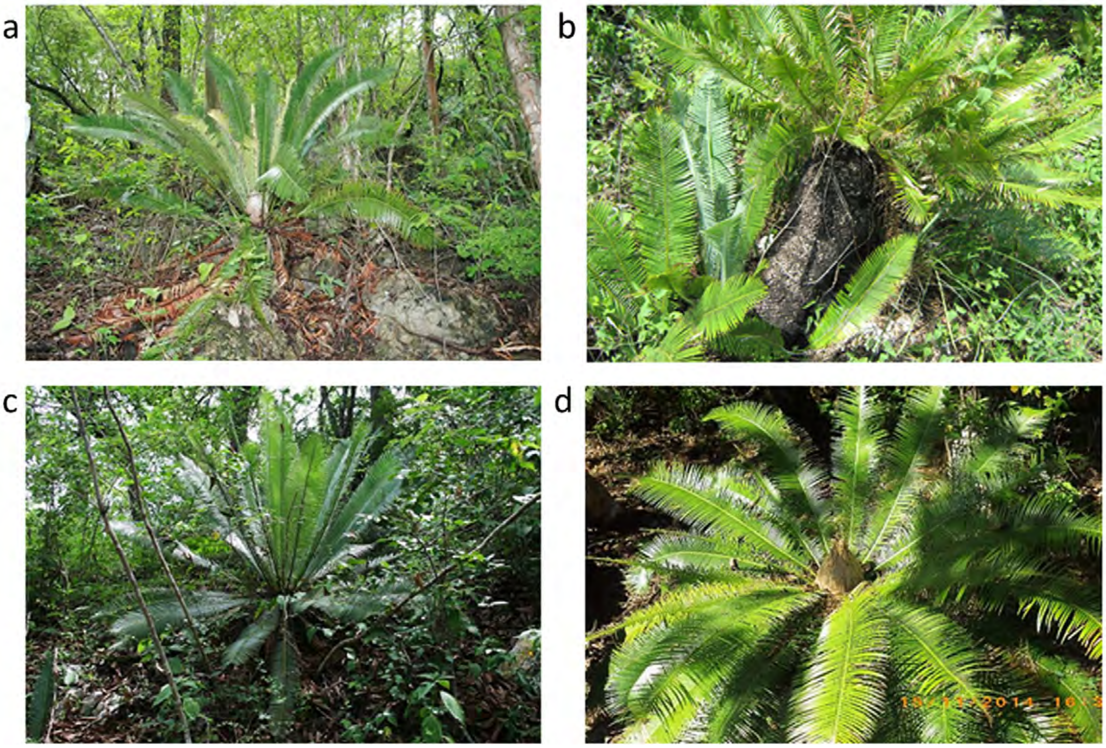

Figure 3. Morphology of *Dioon edule* forms a) "edule"; b) "rioverde"; c) "tamasopo"; d) *D. angustifolium* (photo by María Magdalena Salinas Rodríguez), in their distribution range.

Table 5
Mean (±SE) morphological traits of 15 populations of *Dioon edule* and *D. angustifolium* in their distribution range.

Population	Diameter (cm)	Height (cm)	Leaves number	Leaves No. per flush	Leaf length
E1	24.32 (±3.75)	42.35 (±8.05)	17.14 (±3.72)	3.85 (0.55)	106.29 (±11.48)
E2	31.75 (±4.8)	43.25 (±5.82)	43.75 (±10.9)	4.75 (±0.47)	107.775 (±5.52)
E3	25.25 (±1.09)	49.81 (±6.63)	24.43 (±2.41)	10.5 (2.02)	104.87 (±3.37)
RV1	21.81 (±4.89)	34.55 (±5.96)	-	3.7 (0.3)	82.71 (±6.03)
RV2	15.16 (±0.92)	22.41 (±5.08)	12.25 (±1.85)	3.58 (±0.52)	75.39 (±5.59)
RV3	20.28 (±0.99)	33.76 (±3.14)	21.2 (±1.88)	5.76 (±1.0)	90.29 (±4.8)
RV4	18.12 (±1.41)	30.3 (±5.73)	20.26 (±2.49)	7.04 (±2.06)	70.93 (±3.38)
T1	17.78 (±0.48)	27.83 (±1.8)	17.88 (±1.45)	-	62.86 (±18.8)
T2	25.04 (±0.61)	35.6 (±2.39)	10.5 (±1.35)	4.52 (±0.63)	57.76 (±5.03)
T3	23.83 (±1.67)	41.88(±6.64)	21.22 (±4.46)	8.6 (±1.92)	98 (±22.0)
T4	21.5 (±1.23)	64.83 (±5.35)	20.5 (±3.01)	-	118.3 (±4.59)
T5	21 (±0.41)	42.75 (±2.24)	17.35 (±1.03)	3.46 (±0.31)	91.9 (±1.63)
A1	18.13 (±1.71)	20.93 (±4.72)	22.13 (±1.50)	8.8 (±1.0)	65.54 (±6.87)
A2	18.33 (±2.71)	28.16 (±4.48	22 (±4.46)	8.58 (±1.22)	65.22 (±8.24)
A3	9.25 (±3.09)	6.6 (±4.06)	15.6 (±3.38)	5.8 (±1.24)	48.95 (±12.37)

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influence the phenotypic differences among the forms are precipitation, physiography and vegetation. The correlation analysis showed a moderate negative linear relationship between plant height and latitude (r = -0.538, $p < 0.05$) and a moderate positive relationship between leaf length and annual precipitation (r = 0.538, $p < 0.05$). Likewise, there are moderate negative linear relationships between annual precipitation and elevation (r = -0.577, $p < 0.05$) and latitude (r = -0.520, $p < 0.05$), but a moderate positive relationship with longitude (r = 0.636, $p < 0.05$).

Table 6
Statistical differences between population pairs for 5 morphological traits.

Morphological traits	H	P
Stem diameter	91.05	2.4e-13
Total height	71.93	8.596e-10
Leaves number	42.265	5.927e-05
Leaves No. per flush	42.846	2.398e-05
Leaf length	78.914	4.497e-1

Table 7
Environmental features contribution to the sites where the populations grow.

Environmental variable	Contribution (%)	Permutation importance
Annual precipitation (mm)	52.3	14.5
Slope (%)	31.1	33.9
Vegetation	12.4	43.0
Geology	0.8	4.5
Soil	0.0	0.0
Annual mean temperature (°C)	0.0	0

Discussion

The results of our study highlight the phenotypic variation of *Dioon edule* populations in the latitudinal gradient mentioned by Whitelock (2004), as well as the altitudinal gradient. The inclusion of more populations in the sample allowed us to confirm the “rioverde” and “edule” forms, as well as to propose the new “tamasopo” form. The fact that *D. angustifolium* presents a large proportion of individuals that share morphological traits with *D. edule* in the “tamasopo”, “rioverde” and “edule” forms, supports recent studies showing that *D. angustifolium* do not form a monophyletic group and individuals are nested within *D. edule* populations (Dorsey et al., 2018; Gutiérrez-Ortega, Salinas-Rodríguez et al., 2018). However, the similarities of the morphological traits of some populations of the “rioverde” and “tamasopo” forms with *D. angustifolium* allow us to suggest the presence of the latter in San Luis Potosí, but this will only be resolved when corresponding genetic studies are carried out.

The morphological traits range of the sampled individuals are considerably smaller than those described by Whitelock (2004), which may be due to a greater number of individuals evaluated in several populations, increasing the data variation. Likewise, *D. edule* stems bend or break when they fall to the ground due to the weight of the reproductive structures and are covered by the ground. The leaf length and plant height varied more across latitude than across elevation. Northern populations are subject to lower annual precipitation than southern populations (1:2), but higher interannual variation with 6 to 8 months of dry season, leading to greater phenotypic plasticity. Other studies about intraspecific phenotypic variation along gradients have shown a similar pattern of phenotypic plasticity associated to variation in precipitation across latitude than elevation (Jonas & Geber, 1999).

The results confirmed that precipitation is the variable with the greatest influence on the phenotypic variation in *Dioon edule* forms in San Luis Potosí, as mentioned in a previous study for *Dioon* species (Gutiérrez-Ortega, Salinas-Rodríguez et al., 2018). The annual precipitation is lower at higher latitude and elevation following an aridification pattern, suggesting that the aridification promoted the diversification of the *Dioon edule* complex. However, a previous study (Dorsey et al., 2018) suggests that *D. edule* complex diversification is more consistent with fragmentation of a widespread ancestor or long-distance dispersal. The intraspecific phenotypic variability is associated with adaptations to environmental conditions derived from the isolation of populations, especially after the appearance of large mountain ranges, as well as to the reduction of genetic flow between populations (de Luca et al., 1982; Whitelock, 2004). As found in other studies, the intraspecific traits variation among and within populations, is due to genetic variation and phenotypic plasticity (Souza et al., 2018). Thus, the emergence of new abiotic conditions such as the effects of climate change are not only threats to the species, but also a trigger of biodiversity, causing natural selection pressures that can promote adaptations (Gutiérrez-Ortega, Salinas-Rodríguez et al., 2018). Our study agrees that the variation of intraspecific traits is a relevant mechanism by which individuals can cope with environmental variations and could avoid local extinctions under climatic change (Souza et al., 2018).

The populations of *Dioon edule* studied were classified into the 3 forms proposed by Whitelock (2004): *D. angustifolium* form "angustifolium", and *D. edule* forms "edule" and "rioverde", and the new form "tamasopo". The forms "tamasopo" and "rioverde" present intermediate values between *D. edule* and *D. angustifolium*, with 63% of the individuals classified as "tamasopo". Our results suggest the presence of *D. angustifolium* in San Luis Potosí, but genetic studies must be carried out to corroborate it and find out if hybridization has taken place. The variables that define the distribution of the populations are vegetation type, slope inclination and annual precipitation.

Acknowledgements

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References

Bonta, M., Pulido, M. T., Vargas, T., Vite-Reyes, A., Vovides, A. P., & Cibrián-Jaramillo, A. (2019). Ethnobotany of Mexican and northern Central American cycads (Zamiaceae). *Journal of Ethnobiology and Ethnomedicine*, *15*, 1–34. https://doi.org/10.1186/s13002-018-0282-z

Chávez-Acuña, I. J. (2010). *Análisis estructural de dos poblaciones de* Dioon edule *Lindl. (Zamiaceae) en comunidades indígenas y mestizas de la región xi'iuy de La Palma, S.L.P.: implicaciones ecológicas y culturales (Thesis)*. Universidad Autonóma de San Luis Potosí. San Luis Potosí, Mexico.

de Luca, P., Sabato, S., & Vázquez-Torres, M. (1982). Distribution and Variation of *Dion edule* (Zamiaceae). *Brittonia*, *34*, 355–62. https://doi.org/10.2307/2806710

Dorsey, B. L., Gregory, T. J., Sass, C., & Specht, C. D. (2018). Pleistocene diversification in an ancient lineage: a role for glacial cycles in the evolutionary history of *Dioon* Lindl. (Zamiaceae). *American Journal of Botany*, *105*, 1–19. https://doi.org/10.1002/ajb2.1149

González, D., Vovides, A., & Bárcenas, C. (2008). Phylogenetic relationships of the neotropical genus *Dioon* (Cycadales, Zamiaceae) based on nuclear and chloroplast DNA sequence data. *Systematic Botany*, *33*, 229–236. https://doi.org/10.1600/036364408784571699

González-Astorga, J., Vovides, A. P., & Iglesias, C. (2003). Morphological and geographic variation of the cycad *Dioon edule* Lindl. (Zamiaceae): ecological and evolutionary implications. *Botanical Journal of the Linnean Society*, *141*, 465–470. https://doi.org/10.1046/j.1095-8339.2003.00155.x

Gutiérrez-Ortega, J. S., Salinas-Rodríguez, M. M., Martínez, J. F., Molina-Freaner, F., Pérez-Farrera, M. A., Vovides, A. P. et al. (2018). The phylogeography of the cycad genus *Dioon* (Zamiaceae) clarifies its Cenozoic expansion and diversification in the Mexican transition zone. *Annals of Botany*, *121*, *535*–548. https://doi.org/10.1093/aob/mcx165

Gutiérrez-Ortega, J. S., Yamamoto, T., Vovides, A. P., Pérez-Farrera, M. A., Martínez, J. F., Molina-Freaner, F. et al. (2018). Aridification as a driver of Biodiversity: a case study for the cycad genus *Dioon* (Zamiaceae). *Annals of Botany*, *121*, 47–60. https://doi.org/10.1093/aob/mcx123

Hijmans, R. J. (2012). Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology*, *93*, 679–688. https://doi.org/10.1890/11-0826.1

INEGI (Instituto Nacional de Estadística y Geografía). (2013). Continuo de elevación mexicano (CEM), representación visual y matemática de los valores con respecto al nivel del mar escala 1:50 000 versión 3.0. http://www.beta.inegi.org.mx/temas/mapas/relieve/continental/

Jonas, C. S., & Geber, M. A. (1999). Variation among populations of *Clarkia unguiculate* (Onagraceae) along altitudinal and latitudinal gradients. *American Journal of Botany*, *86*, 333–343. https://doi.org/10.2307/2656755

Rubio-Méndez, G. (2010). *Estructura poblacional de* Dioon edule *en la Sierra Madre Oriental de San Luis Potosí (Thesis)*. Universidad Autónoma de San Luis Potosí. San Luis Potosí, Mexico.

Souza, M. L., Duarte, A. A., Lovato, M. B., Fagundes, M., Valladares, F., & Lemos-Filho, J. P. (2018). Climatic factors shaping intraspecific leaf trait variation of a neotropical tree along a rainfall gradient. *Plos One*, *13*, e0208512. https://doi.org/10.1371/journal.pone.0208512

Tristán-Martínez, E. (2012). *Aprovechamiento alimentario del chamal (*Dioon edule *Lindl.) en comunidades xi'iuy (pame) de los municipios de Tamasopo, Rayón y Santa Catarina en el estado de San Luis Potosí (Thesis)*. Universidad Autónoma de San Luis Potosí. San Luis Potosí, Mexico.

Whitelock, L. M. (2004). Variation in the Mexican Cycad *Dioon edule* (Zamiaceae). *Botanical Review*, *70*, 240–49. https://doi.org/10.1663/0006-8101(2004)070[0240:VITMCD]2.0.CO;2

Yáñez-Espinosa, L. (2006). *Las cycadas. Biología y conservación en México*. México D.F.: Universidad Autónoma Chapingo.