



ECOLOGICAL NICHE OF SEMIDOMESTICATED POPULATIONS OF *Capsicum pubescens* RUIZ & PAV. BASED ON ACCESSIONS FROM VERACRUZ, MEXICO

NICHO ECOLÓGICO DE POBLACIONES SEMIDOMESTICADAS DE *Capsicum pubescens* RUIZ & PAV. CON BASE EN ACCESIONES DE VERACRUZ, MÉXICO

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SUMMARY

To be able to cultivate a wild species it is necessary to modify the genetic scheme resulting from natural selection processes to one adapted to human-managed conditions, it implies to detect geographic areas similar to those where the species originated. This study analyzes a model of potential geographic areas for *Capsicum pubescens* Ruiz & Pav adaptation, aiming to detect the appropriate ecological niche conditions in Mexico, and to describe the relationships between the environment and the morphological characteristics of the fruit. The recent maximum entropy modeling algorithm (MaxEnt) was used to model the niche of *C. pubescens* within an important region in Central Veracruz, Mexico. A total of 44 sites of presence and four bioclimatic variables were used to detect adequate niches for the species; also, a partial least squares regression analysis was performed by combining presence sites, bioclimatic variables and morphological characteristics of the fruit. A final suitability map was built identifying the areas suitable for *C. pubescens* growth. The contributions of the predictor variables to the model were annual rainfall (Bio12) 43.9 %, potassium layer (K) 23 %, altitude (DEM) 22.3 % and mean annual temperature (Bio1) 10.7 %, with a value of area under the curve of 99.7 %. The partial minimum squares corroborated the importance of covariables, which intervene in the expression of morphological characteristics of the fruit, helping to better understand the relationships between species and the environment. Areas not yet explored had occurrence values over 90 %, mainly in the mountainous regions of Chihuahua, Tamaulipas, Nuevo Leon, and the Santa Martha Sierra in southern Veracruz. A group of outstanding accessions was identified that could serve as the basis to initiate a breeding program for this species.

Index words: *Capsicum pubescens*, bioclimatic gradients, deductive approach, maximum entropy, plant species management, species distribution models.

RESUMEN

Para cultivar una especie silvestre es necesario modificar el esquema genético resultante de los procesos de selección natural a uno adaptado a las condiciones manejadas por el hombre, e implica detectar áreas geográficas similares a aquellas donde se originó la especie. En este estudio se analiza un modelo de áreas geográficas potenciales para la adaptación de *Capsicum pubescens* Ruiz & Pav. con el objetivo de detectar las condiciones de nicho

ecológico apropiado, determinar zonas potenciales en México y describir las relaciones entre el medio ambiente y las características morfológicas del fruto. Se utilizó el algoritmo reciente de máxima entropía (MaxEnt) para modelar el nicho de *C. pubescens* dentro de una región de importancia en el centro de Veracruz, México. Se utilizó un total de 44 sitios de presencia y cuatro variables bioclimáticas para detectar nichos adecuados para la especie; así mismo, se realizó un análisis de regresión por mínimos cuadrados parciales (PLS) combinando los sitios de presencia, variables bioclimáticas y características morfológicas del fruto. Se construyó un mapa final de idoneidad identificando las áreas adecuadas para el crecimiento de *C. pubescens*. Las contribuciones de las variables predictoras al modelo fueron precipitación anual (Bio12) 43.9 %, capa de potasio (K) 23 %, altitud (DEM) 22.3 % y temperatura media anual (Bio1) 10.7 %, con valor del área bajo la curva de 99.7 %. Los mínimos cuadrados parciales corroboraron la importancia de las covariables, que intervienen en la expresión de características morfológicas del fruto, ayudando a entender mejor las relaciones entre especies y el medio ambiente. Áreas aún no exploradas arrojaron probabilidades de ocurrencia mayores a 90 %, principalmente en las zonas montañosas de Chihuahua, Tamaulipas, Nuevo León y la Sierra de Santa Martha al sur del estado de Veracruz. Se identificó un grupo de accesiones sobresalientes que podrían servir como base para iniciar un programa de mejoramiento genético en esta especie.

Palabras clave: *Capsicum pubescens*, enfoque deductivo, gradientes bioclimáticos, manejo de especies de plantas, máxima entropía, modelos de distribución de especies.

INTRODUCTION

Genetic resources of wild species related to cultivated plants constitute a gene pool that can help to solve agricultural problems (Hernández-Verdugo *et al.*, 1998). To be able to cultivate a wild species it is necessary to modify the genetic scheme resulting from natural selection processes to one adapted to human-managed conditions (Hernández, 1985). Such manipulation allows man to adapt biological diversity to the needs of human society (Casas and Caballero, 1995) and is carried out through artificial selection, which in parallel also results in the evolutionary

process of domestication (Mastretta-Yanes *et al.*, 2019). For Gepts and Papa (2003), domestication is a continuous genetic selection process exercised by humans during the adaptation of plants and animals; this process generated morphological, physiological and genetic changes known as domestication syndrome (Gepts, 2005; Pickersgill, 2007).

Crops vary within and between species in their degrees of domestication. All known accessions of *Capsicum pubescens* have large fruits that have lost their dispersal mechanism, and this species occurs only in cultivation. The four other species of domesticated chili pepper each includes a range of variation from wild peppers, through cultivated peppers with somewhat larger fruits that are still capable of natural dispersal, to fully domesticated peppers with large fruits that remain firmly attached to the parent plant after maturity. Clement (1999) proposed two intermediate categories, incipiently domesticated and semidomesticated, to cover the spectrum of changes resulting from human interactions with species of tree fruits in Amazonia. Semidomesticated also fits the situation described by Casas *et al.* (1998) for *Stenocereus stellatus*, a giant cactus exploited and cultivated for its fruit in the Tehuacan Valley of Mexico. Casas (1998) considered that such changes in allele frequencies resulting from human selection constitute at least incipient domestication.

The *Capsicum* genus includes around 25 species belonging to the Solanaceae family (Meckelmann *et al.*, 2015); of these, five species have been domesticated in at least two geographical regions of the new world (*C. annum* and *C. frutescens* in Mesoamerica; *C. baccatum*, *C. pubescens*, and *C. chinense* in South America) (Loaiza-Figueroa *et al.*, 1989; Pickersgill, 2007). Of the five domesticated species, *C. pubescens* Ruiz & Pav. is one of the main native species cultivated in the Andes (DeWitt and Bosland, 2009). Recent studies indicate that its cultivation and domestication began approximately 6000 years BC in the mid and high regions of Peru and Bolivia, at altitudes ranging from 1300 to 3000 masl (Ruiz and Pavon, 1799). *C. pubescens* is commonly known as "Rocoto" in Peru and "Locoto" in Bolivia (Meckelmann *et al.*, 2015), and as "Manzano" and "Cera" in Mexico (Pérez-Grajales *et al.*, 2004), due to its shape and appearance.

In Mexico, *C. pubescens* is distributed throughout the temperate areas of the states of Puebla, Michoacan, Mexico, Oaxaca and Veracruz. It is generally grown in production systems associated with fruit trees such as coffee (*Coffea arabica* L.), banana (*Musa* spp. L.), apple (*Malus domestica* Borkh.), peach (*Prunus persica* (L.) Batsch.), avocado (*Persea americana* Mill.), as well as some lumber species like cedar (*Cedrus* spp.) and ilite (*Alnus acuminata* Kunth.),

among others. *Capsicum pubescens* is a perennial plant with purple flowers and hard-headed black seeds (Leyva-Ovalle *et al.*, 2018). Its growth habit can be determined or undetermined, with trichomes in stems and leaves (Pérez-Grajales *et al.*, 2004). Fruits vary greatly in size, shape and color (DeWitt and Bosland, 2009; Leyva-Ovalle *et al.*, 2018; Rick, 1950; Yamamoto *et al.*, 2013).

The fruits are rich in vitamins (A, C and B6), β -carotene, flavonoids, capsanthin, among others (Liu *et al.*, 2013); also, the antioxidant properties of carotenoids protect against diverse heart diseases and cancer (Rodríguez-Burruezo *et al.*, 2009). Likewise, the fruits can be dehydrated and used as a condiment in different dishes (Obob *et al.*, 2007). Because of this, the consumption of this fruit has grown in recent years as a consequence of increasing Latin American populations in the United States of America and Europe, as well as the increasing interest in functional foodstuffs (Pérez and Castro, 2008; Rodríguez-Burruezo *et al.*, 2009).

There are few papers on the cultivation and distribution of *C. pubescens*, especially in Central America, where it has diversified. The influence of environmental, geographical, and soil conditions associated with its ecological niche is unknown; therefore, this study was carried out to elucidate the ecological niche conditions, to determine potential growing zones in Mexico, and to describe the possible relationships between the environment and the morphological characteristics of the fruit, as revealed by its current distribution.

MATERIALS AND METHODS

Study sites and data collection

The field work was carried out from October 2016 to March 2017 in 13 municipalities of the central region of the state of Veracruz, Mexico (Table 1, Figure 1). A total of 44 accessions of *C. pubescens* were obtained; the geographical coordinates of each site were registered to be used as occurrences to build the model.

Characterization of *C. pubescens* fruits

Fifteen fruits at harvest maturity stage were collected from each site. Each of the fruits was morphologically characterized based on descriptors of the International Plant Genetic Resources Institute (IPGRI, 1995). Traits registered were length fruit (Lenfru) in cm, width fruit (Widfru) in cm, weight fruit (Wefru) in g, pedicel length (Lenped) in mm, wall thickness (Thfru) in mm, placental length (Lenpla) in cm, and number of seeds (Numsed).

A multivariate technique of partial least squares

Table 1. Accessions evaluated in this study.

Id	Accession	Municipality	Origin	Farmer name	Altitude	Latitude	Longitude
1	MEXUVDC1	Coscomatepec	Dos caminos	Miguel Milian Ramos	1454	19.04419	-97.03058
2	MEXUVCAL1	Calcahualco	Calcahualco	Roberto Reyes M	1762	19.12128	-97.08269
3	MEXUVCAL2	Calcahualco	Calcahualco	Marcelino Espinoza de la Cruz	1680	19.12000	-97.07697
4	MEXUVCAL3	Calcahualco	Calcahualco	Marcelino Espinoza de la Cruz	1708	19.11708	-97.07697
5	MEXUVCV1	Calcahualco	Cruz Verde	Estanislao García	1927	19.13417	-97.10750
6	MEXUVCV2	Calcahualco	Cruz Verde	Remigia Ortiz Hernández	1923	19.13306	-97.10556
7	MEXUVTE1	Alpatlahuac	Teacalco	Manuela Martínez	2570	19.11417	-97.16556
8	MEXUVC01	Alpatlahuac	Cocalcingo	Amalia Martínez	1990	19.09272	-97.10944
9	MEUVTL1	Alpatlahuac	Tlatelpa	David Dorantes	1799	19.11667	-97.08528
10	MEXUVTEPE1	Zongolica	Tepetitlanapa	José Ismael Vallejo Chimalgua	1523	18.64172	-97.01292
11	MEXUVTEX1	Texhuacan	Texhuacan	Matilde Tepole Xalamihua	2019	18.62193	-97.04673
12	MEXUVBP1	Mixtla de Altamirano	Barrio Primero	Evaristo Mayahua Flores	1678	18.60077	-96.99268
13	MEXUVLA1	Texhuacan	La Aposteca	Félix Cano Hernández	1431	18.61490	-97.00960
14	MEXUVCG1	Chocamán	Colonia la Garita	Anonymous	1332	19.00816	-97.02664
15	MEXUVBJ1	Coscomatepec	Barranca de Jamapa	María Antonia Tentle Morales	1365	19.09937	-97.03216
16	MEXUVTEP1	Huatusco	Tepampa	Francisco Huerta Ballona	1716	19.13524	-97.02220
17	MEXUVTEP2	Huatusco	Tepampa	Lázaro Huerta Rodríguez	1743	19.14219	-97.02421
18	MEXUVTEN1	Huatusco	Tenejapa	Anonymous	1404	19.13699	-97.00624
19	MEXUVTEN2	Huatusco	Tenejapa	María Luisa Sánchez Marinero	1373	19.13587	-97.00200
20	MEXUVTZ1	Tehuipango	Tzacoala Primero	Agustina Calihua Panzo	2090	18.53895	-97.07902
21	MEXUVTLA1	Tehuipango	Tlalchichilco	Pascuala Panso Chipahua	2369	18.54041	-97.05128
22	MEXUVTLA2	Tehuipango	Tlalchichilco	Pascuala Panso Chipahua	2369	18.54041	-97.05128
23	MEXUVTE2	Alpatlahuac	Teacalco	Alejandro Gómez	1825	19.10950	-97.09961
24	MEXUVTL2	Alpatlahuac	Tlatelpa	David Dorantes	1803	19.11697	-97.08578
25	MEXUVC02	Alpatlahuac	Cocaltzingo	María Martínez	1968	19.09156	-97.10953
26	MEXUVBV1	Tepatlxco	Buena Vista	Roberto Sánchez Hernández	1457	19.04153	-96.87311
27	MEXUVTE3	Alpatlahuac	Teacalco	Gerardo Torres	1825	19.10983	-97.09953
28	MEXUVCV3	Calcahualco	Cruz Verde	Anonymous	1934	19.13447	-97.10783
29	MEXUVCV4	Calcahualco	Cruz Verde	Vicente Espejel	1939	19.13614	-97.10978
30	MEXUVTER1	Calcahualco	Terrero	Rosalino	1913	19.13192	-97.10344
31	MEXUVCV5	Calcahualco	Cruz Verde	Remigia	1940	19.13611	-97.10975
32	MEXUVTER2	Calcahualco	Terrero	Diocleciana	1914	19.13194	-97.10333
33	MEXUVTER3	Calcahualco	Terrero	Serafina	1914	19.13192	-97.10339
34	MEXUVTET1	Coscomatepec	Tetlxco	Cirilo Roque	1678	19.03711	-97.06344
35	MEXUVTET2	Coscomatepec	Tetlxco	Juan Alejo Rosales	1683	19.03692	-97.06258
36	MEXUVHU1	Soledad Atzompa	Huixtitla	Leticia López Flores	2514	18.71276	-97.16385

Table 1. Continues.

Id	Accesion	Municipality	Origin	Farmer name	Altitude	Latitude	Longitude
37	MEXUVNE1	Camerino Z. Mendoza	Necoxtla	Margarita Pérez Flores	2045	18.77791	-97.15361
38	MEXUVCU1	Tehuipango	Cuauyolotitla	Gines Panzo Panzo	2387	18.51914	-97.06378
39	MEXUVCU2	Tehuipango	Cuauyolotitla	Gines Panzo Panzo	2408	18.51906	-97.06331
40	MEXUVTZ2	Tehuipango	Tzacuala Primero	Anonymous	2108	18.53874	-97.08197
41	MEXUVTEH1	Tehuipango	Tehuipango	Anonymous	2393	18.51947	-97.05444
42	MEXUVVH1	Tlaquilpa	Vista Hermosa	Lucía Clemente Sandoval	2592	18.59497	-97.12811
43	MEXUVCA1	Tlaquilpa	Capillatitla	Jerónima Rosales	2410	18.61050	-97.11708
44	MEXUVDA1	Tlaquilpa	Desviación Atempa	Félix	2226	18.60092	-97.10422

regression (PLSR) was applied, which allows describing the populations considering several morphological characteristics simultaneously, without failing to consider the relationship existing between them. This analysis is useful to predict a set of dependent variables (morphological characteristics) from a set of predictor variables (bioclimatic layers) (Gaviria *et al.*, 2016).

Species distribution model

The species distribution model (SDM) was used to predict suitable areas for *C. pubescens* in places where it occurs. In this model, the locations of the current known distribution of *C. pubescens* are grouped. Four climatic prediction variables were selected: mean annual temperature (Bio1), annual rainfall (Bio12), altitude (DEM), and a potassium (K) layer as soil property (Bugarín-Montoya *et al.*, 2002; Cruz-Cárdenas *et al.*, 2014). These variables were taken from the spatial databases from <http://www.worldclim.org> (Hijmans *et al.*, 2005). The estimation of the ecological niche was carried out through the maximum entropy algorithm, MaxEnt® Ver. 3.3 (Phillips *et al.*, 2006). Once the potential distribution map was obtained, it was exported to the ArcMap® Versión 10.5.1 software (ESRI, 2017) for contextualization and image manipulation. The quality of the model was evaluated with > 0.9 values of the area under the curve (AUC), which characterizes the performance of the model. The result is a graph output that shows the discrimination capacity of a given presence (sensitivity) versus the discrimination capacity of a given absence (specificity) (Phillips *et al.*, 2004).

RESULTS AND DISCUSSION

***C. pubescens* presence sites**

Forty-four sites were identified with the presence of *C. pubescens* in the studied area. Using the coordinates,

a distribution map was generated and two regions, A and B, were identified (Figure 1). Region A included the municipalities of Zongolica, Tlaquilpa, Texhuacan, Mixtla de Altamirano, Camerino Z. Mendoza, Soledad Atzompa and Tehuipango; region B included the municipalities of Calchahuaco, Alpatlahuac, Chocamán, Coscomatepec, Huatusco and Tepatlaxco.

Region A has a *Cf* type climate, temperate humid with rains throughout the year, exceeding 2200 mm per year (> 18 % of winter rain), with little thermal oscillation (5 to 7 °C). Region B possesses a *Cw* type climate, temperate sub-humid with rains in the Summer, with more than 800 mm per year (< 10.2 % of winter rain), with isothermal oscillation range (< 5 °C) (Díaz *et al.*, 2006; García, 2004). Both regions have altitudes ranging from 1300 to 2700 masl, places where the maximum rainfall arises as a result of the discharge of water by warm air masses from the sea (Krasilnikov *et al.*, 2013). They also have an average annual temperature between 5 to 18 °C, while in the coldest month between -3 to 18 °C (García, 2004; SEMARNAT, 2006).

Ecological niche model for *C. pubescens*

The efficiency of the model reached an AUC value over 0.997, indicating that the ability of the model to classify presences was consistent in the prediction of the ecological niche (Baldwin, 2009; Phillips and Dudík, 2008). The results of the test data (P = 0.5) revealed that the model obtained is better than a randomized model, since the curves are located at the upper left corner (Figure 2) and indicate that there is no error of omission (100 % sensibility) and no error of commission (100 % specificity) (Cruz-Cárdenas *et al.*, 2014). These results indicate that the samples were viably taken from the population and that they are truly representative, as there is no ambiguity in the prediction of the ecological niche for *C. pubescens*. In biological terms, the model reflects reliability, providing useful information

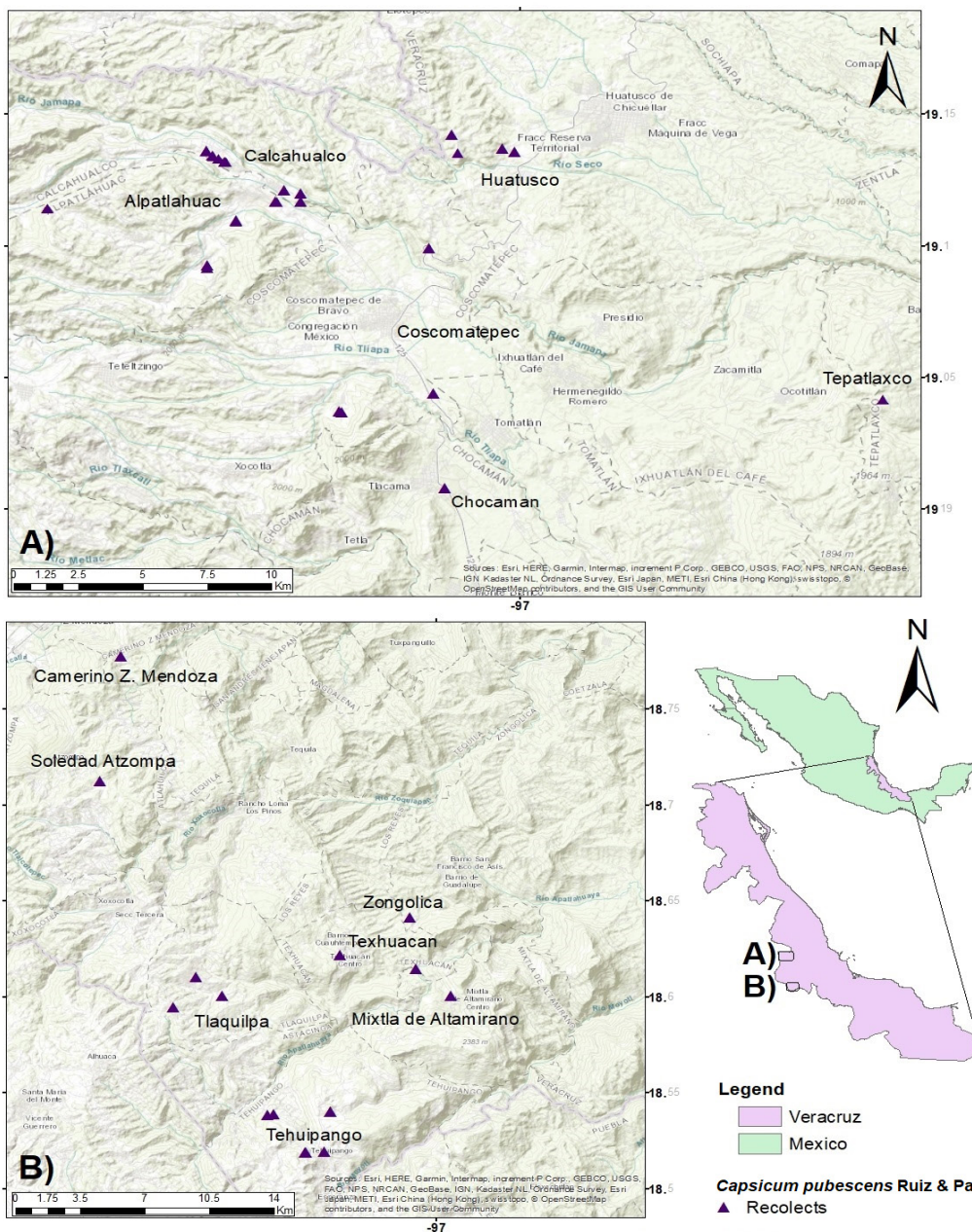


Figure 1. Geographical distribution of 44 *C. pubescens* accessions from the central region of the state of Veracruz, Mexico in two contrasting zones, A and B.

for a breeding program. In this regard, Pearson *et al.* (2007) mentioned that few presences can give enough information for the MaxEnt model to produce acceptable predictions for the distribution of a certain species.

To this regard, the potential distribution of *C. pubescens* shown in the map of Figure 3, reveals that the best conditions of occurrence are found in the mountainous regions of Chiapas, Oaxaca, Puebla, and Hidalgo, Mexico

(Figure 3B); however, a new registry was found in southern Veracruz, at the San Martín Sierra and the Santa Martha Sierra in the Tuxtla region, at an altitude of 1500 masl (Figure 3B). From an ecological standpoint, *C. pubescens* is distributed in temperate regions, which coincide with areas of dense vegetation and subtropical forests. This is consistent with the reports on its distribution and habitat (Yamamoto *et al.*, 2013).

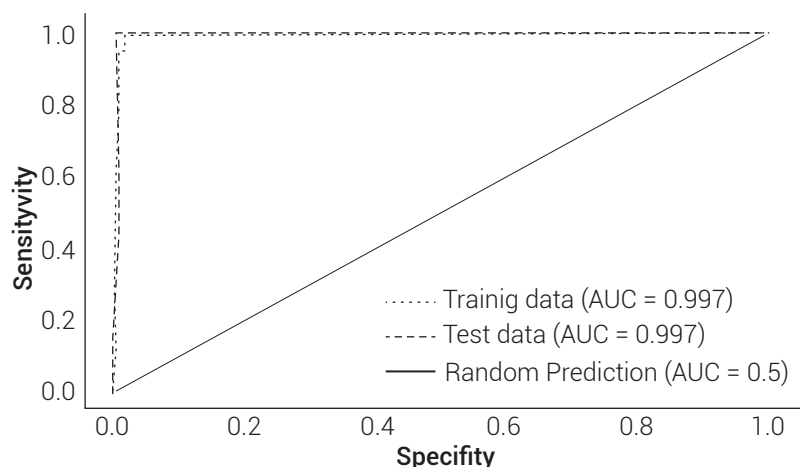


Figure 2. Goodness of fit of the model to estimate the potential distribution of *C. pubescens*.

The model revealed other areas where the presence of *C. pubescens* is unknown (Leyva-Ovalle *et al.*, 2018). These areas showed a restricted habitat potential, like the Sierra Madre Oriental and Sierra Madre Occidental in the states of Tamaulipas, Nuevo Leon and Chihuahua, Mexico, at an altitude gradient between 2200 and 2700 masl (Figure 3A).

According to the analysis of the contribution of each variable provided by the MaxEnt model, it was found that the variables with larger contribution to the model when they are used separately were annual rainfall (Bio12) with 43.9 %, potassium layer (K) with 23 %, altitude (DEM) with 22.3 %, and mean annual temperature (Bio1) with 10.7 %. This suggests that *C. pubescens* achieves good growth and development in temperate zones with high rainfall; however, the presence of low temperatures and frost at higher altitudes may limit its distribution (Soto and Geissert, 2011). Furthermore, the species grows on pyroclastic sediments, in acidic volcanic ash, which explains the high content of K, an element that is highly resistant to weathering (Krasilnikov *et al.*, 2013). On the other hand, the humid conditions in areas where the species grows promote the acidity of the soil (pH = 4.2), and together with their mountainous relief, they cause erosion and loss of nutrients (Krasilnikov *et al.*, 2013; Medina *et al.*, 2010; SEMARNAT, 2006), demonstrating their adaptation even under these conditions; in this sense, the use of ecological niche models contributes to a better understanding of the relationships between species and the environment (Parolo *et al.*, 2008).

Partial least square regression in *C. pubescens*

The least square regression is a technique that generalizes and combines the principal component analysis and the linear regression analysis. It is ideal to predict a set of

dependent variables (e.g. morphological) from a set of predictor variables (e.g. climatological). The covariable with the highest inertia and positively linked to the first axis was mean annual rainfall (Bio12), while negatively it was the availability of potassium (K) in the soil. The covariable positively linked to the second axis was altitude (DEM), while negatively was mean annual temperature (Bio1).

Accessions MEXUVCAL1, MEXUVCAL3, MEXUVTL2, MEXUVBV1, MEXUVCV5 and MEXUVTER3 showed the best values in number of seeds, fruit thickness and peduncle length; also, their expression is better in more humid environments (Figure 4). These accessions were collected in Calchualco, Alpatlahuac, and Tepatlaxco, Veracruz, Mexico, whose altitude ranges from 1400 to 1800 masl and have a mean annual rainfall between 1800 and 2300 mm.

Meanwhile, accessions MEXUVCO1, MEXUVTEX1, MEXUVTZ1, MEXUVTLA2, MEXUVCO2, MEXUVCU2, MEXUVTZ2, MEXUVTEH1 and MEXUVDA1 were segregated, mainly due to the variables altitude (DEM) and potassium (K) as a soil property (Figure 4), they showed high values for fruit weight and width, which agrees with the locations of provenance, as Tehuipango and Alpatlahuac, Veracruz, Mexico, located at 2500 masl. The interactions detected in this dataset are mainly attributed to these two traits, from the ecological standpoint. This clarifies various ecological hypotheses that can contribute to better understand the relationships between environments and genotypes.

The presence of potassium (K) is closely linked to fruit weight, width and length, its presence is related to fruit quality. It is important to mention that the extraction of large amounts of this element is greatly due to the formation and development of fruits, which are the most

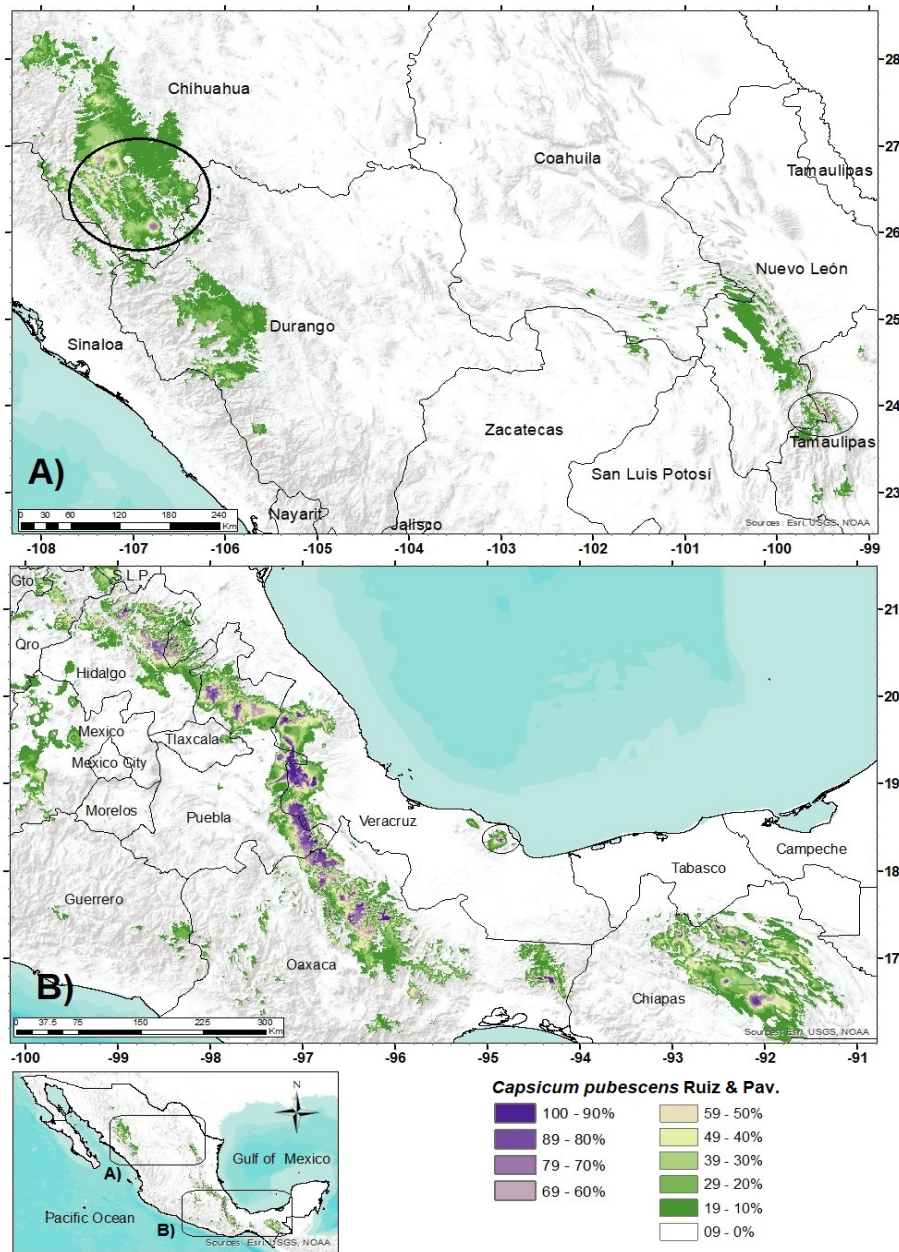


Figure 3. Potential distribution area of *C. pubescens* in Mexico, as predicted by the maximum entropy model (MaxEnt).

demanding organ in *Capsicum*, with values from 70 to 80 % of the total amount extracted from each plant (Bugariń-Montoya *et al.*, 2002).

The opposing projection of the covariables altitude (DEM) and mean annual temperature (Bio1) suggests that the latter changes differentially from one location to another, directly affecting some fruit characteristics. Accessions MEXUVBJ1, MEXUVTEP1, MEXUVTEN2 and MEXUVTET2 showed the lowest values in relation to the length of the placenta, which indicates that this characteristic was

significantly affected by Bio1. According to the mean values of Bio1 registered in the locations where these accessions were collected, the values are above the optimum limits for *C. pubescens* (18 and 25 °C). Pérez and Castro (2008) reported an optimum range from 15 to 22 °C for proper development of *C. pubescens*; moreover, they mentioned that temperatures below 7 °C halt the physiological-metabolic processes in the plant, while temperatures above 32 °C during the critical stage of the crop stimulate abortion of flowers.

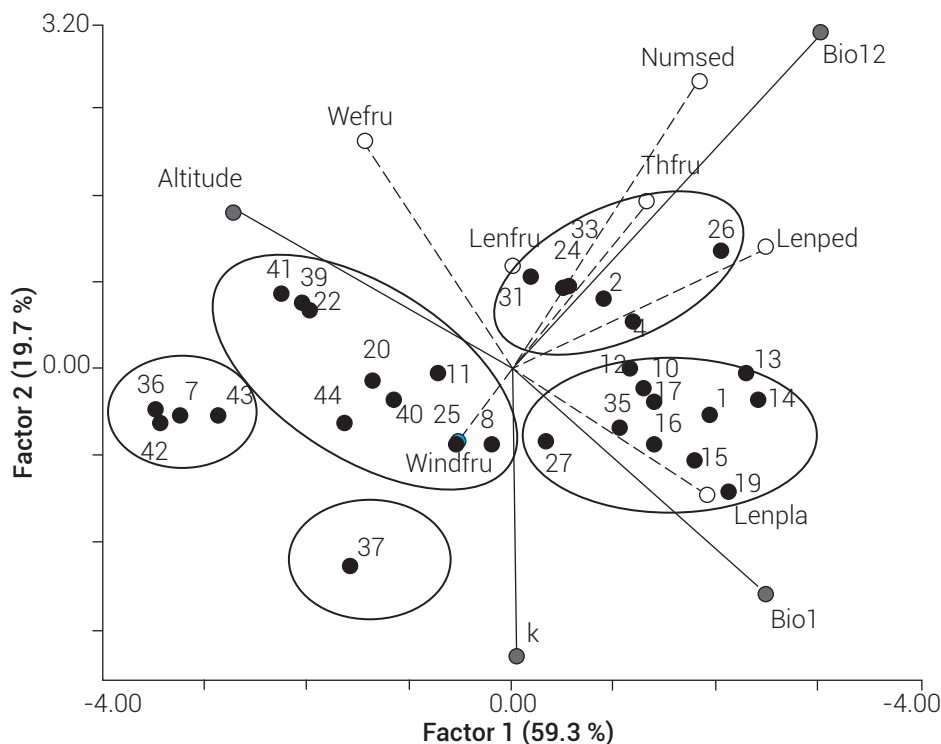


Figure 4. Interaction of 44 accessions of *C. pubescens* and four environmental variables, against a matrix of seven morphological variables of the fruit.

CONCLUSIONS

The distribution model MaxEnt produced probability values > 70 % for the presence of the species. These areas are located in the states of Tamaulipas, Nuevo Leon, Chihuahua and the Santa Martha Sierra in southern Veracruz; nevertheless, it is necessary to carry out exploratory trips to corroborate the presence of the species where it was predicted. Mean annual rainfall (Bio12), mean annual temperature (Bio1), potassium (K), and altitude (DEM) were the most important bioclimatic variables to define specific environments for *C. pubescens*, and they significantly influence the expression of morphological characteristics of the fruit.

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