



Genetic structure of *Platanus mexicana* var. *mexicana* (Platanaceae) in southern Mexico

Estructura genética de *Platanus mexicana* var. *mexicana* (Platanaceae) en el sur de México

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ABSTRACT

Platanus mexicana is a typical species of the tropical cloud forest with a complex biogeographical history. High adaptive radiation and interspecific hybridization have been reported for this species, leading to high genetic variability and low differentiation. However, previous studies have shown that populations in the southern part of the species' distribution in Mexico show different patterns. Therefore, this research aimed at characterizing the genetic structure of three *Platanus mexicana* populations in southern Mexico. The results revealed significant differences between the populations in Oaxaca, Veracruz and Chiapas ($F_{ST} = 0.235 \pm 0.08$), whereas there was evidence of gene flow between the two northwestern populations ($N_m = 1.5$). Bayesian analysis of allele frequencies showed high selection pressure in Veracruz. Furthermore, the alleles that shifted away from the neutral model were overrepresented in Chiapas. The Oaxaca population had the highest genetic variability values ($H_e = 0.25$; $P = 68.7$), whereas the Chiapas

population displayed the highest differentiation ($Nei = 0.134$). Considering the biogeographical history and topographic heterogeneity of the region, the results suggest three differentiation processes: presence of a climate refugium in Oaxaca, allopatry between Veracruz and Oaxaca, and vicariance in Chiapas.

Keywords: Allopatry; Bayesian analysis; Climate refugium; Natural selection; Sycamore; Vicariance.

RESUMEN

Platanus mexicana es una especie característica del bosque de niebla con una compleja historia biogeográfica. Se ha reportado alta radiación adaptativa e hibridación interespecífica en esta especie, lo cual está asociado con alta variación genética y poca diferenciación. Sin embargo, estudios previos han mostrado diferencias significativas entre las poblaciones al sur de su distribución en México. Por tanto, este trabajo tiene como objetivo caracterizar la estructura genética entre tres poblaciones de esta especie en el sur del país. Los resultados muestran diferencias significativas entre poblaciones de Oaxaca, Veracruz y Chiapas ($F_{ST} = 0.235 \pm 0.08$) aunque existe evidencia de flujo genético entre las dos poblaciones del noroeste ($Nm=1.5$). El análisis bayesiano de frecuencias alélicas mostró alta presión de selección en Veracruz. Además, los mismos alelos que se alejan del modelo neutral están sobrerrepresentados en Chiapas. La mayor variabilidad genética se encontró en Oaxaca ($He = 0.25$, $P = 68.7$) y la población con mayor diferenciación genética fue Chiapas ($Nei = 0.134$). Considerando la historia biogeográfica y heterogeneidad topológica, los resultados obtenidos sugieren tres procesos de diferenciación: la presencia de un refugio climático en Oaxaca, alopatria entre Veracruz y Oaxaca, y vicarianza en Chiapas con el resto de las poblaciones.

Palabras clave: Alopatria; Análisis bayesiano; Haya; Refugio climático; Selección natural; Vicarianza.

1. INTRODUCTION

While the Platanaceae botanical family was abundant and diverse during the Cretaceous and early Tertiary, it is currently represented by a single genus (*Platanus*) including seven species, five of which are found in North America. Following a dry episode during the Tertiary, the five North American species were segregated into the western (two species) and eastern (three species) parts of the continent, the genus being virtually absent in the center (Nixon & Poole, 2003). Later on, during the Pleistocene, population decline of some species has been attributed to glaciations, as exemplified by low genetic diversity in *Platanus occidentalis* (Besnard *et al.*, 2002; Feng *et al.*, 2005). Molecular data suggests that *Platanus rzedowskii* emerged as an hybrid of *P. mexicana* and *P. occidentalis* favored by the cyclic expansion and reduction of the latter species' distribution range during Pleistocene glaciations (Nixon & Poole, 2003; Feng *et al.*, 2005; Grimm & Denk, 2008), which affected gene flow (Hampe & Jump, 2011).

Different mechanisms can contribute to gene flow in plants, eventually leading to hybridization. Studies with molecular markers have shown a high level of

hybridization in the genus *Platanus*; examples of hybrids are *P. densicoma*, *P. hispanica*, and *P. x acerifolia* (Besnard *et al.*, 2002; Grimm & Denk, 2008). In addition, horizontal gene flow has been shown to occur between wild populations of *P. mexicana* (var. *mexicana* and var. *interior*), *P. occidentalis* (var. *palmeri* and var. *occidentalis*) and *P. rzedowskii*.

Genetic variability is affected by climate and landscape features, which can combine to create so-called “climate relicts”. Mexico is a country with wide variations in topography and physiography, creating different microclimates ideal for speciation (Sosa *et al.*, 2018). Temperate genera such as *Carpinus*, *Clethra*, *Cornus*, *Liquidambar*, *Pinus* and *Platanus* can be found at mid-to-high altitudes in Mexico, the elevation gradient providing a barrier to gene flow with Neotropical species located at lower altitudes (Graham, 1999; Rico, 2019). The biogeographical history of Mexico suggests that mountains might have been climate refugia during the Pleistocene, especially in the Balsas Basin (Luna-Vega, 2008). This region includes the western part of the states of Tlaxcala, Puebla, Oaxaca and Guerrero. To the northwest, it is separated from the Central Plateau by the Trans Mexican Volcanic Belt. To the southeast, it is separated from the High Grijalva Basin by the Sierra de Juárez. To the northeast, it is separated from the Papaloapan Basin by the Sierra Norte de Oaxaca (Fig. 1).

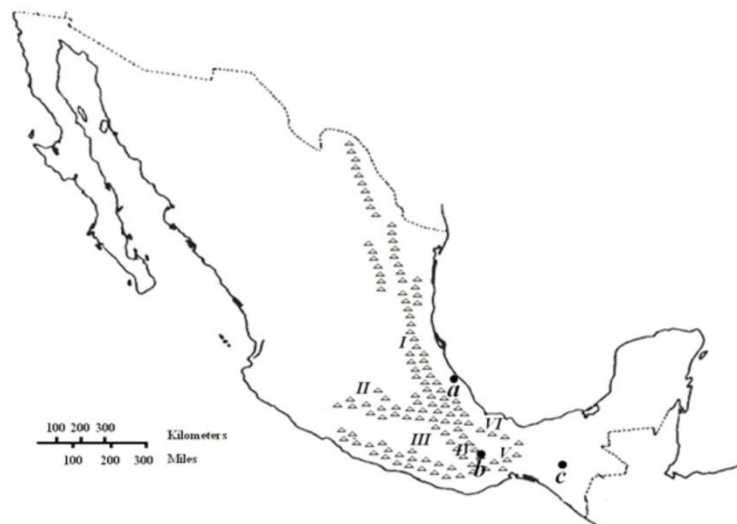


Fig. 1. Main topographic barriers in southern Mexico: I) Sierra Madre Oriental; II) Trans Mexican Volcanic Belt; III) Balsas Basin; IV) Sierra de Juárez; V) Upper Grijalva Basin; VI) Papaloapan Basin. Studied *Platanus mexicana* var. *mexicana* populations: a) Colipa, Veracruz; b) San Juan Comaltepec, Oaxaca; c) Ixtapa, Chiapas.

Fig. 1. Principales barreras topográficas en el sur de México: I) Sierra Madre Oriental; II) Faja Volcánica Transversal; III) Cuenca del balsas; IV) Sierra de Juárez; V) Cuenca superior de Grijalva; VI) Cuenca del Papaloapan. Poblaciones de *Platanus mexicana* var. *mexicana* estudiadas: a) Colipa, Veracruz; b) San Juan Comaltepec, Oaxaca; c) Ixtapa, Chiapas.

Populations of *Platanus mexicana* var. *interior* are present from the southeast of Tamaulipas to the Balsas Basin, through the states of San Luis Potosí, Querétaro and Hidalgo in the Sierra Madre Oriental. *P. mexicana* var. *mexicana* is found from

north of Veracruz (Pánuco) on the coastal side of the Sierra Madre Oriental, south to Guatemala, through the states of Hidalgo, Puebla and Oaxaca (Denk *et al.*, 2012). The distinction between the *interior* and *mexicana* varieties is still controversial. While Denk *et al.* (2012) suggest they belong to a unique species with high phenotypic plasticity, Nixon & Poole (2003) argue there is enough morphological distinction to warrant considering them as two different species. Plastid DNA sequencing and nuclear SNP (single nucleotide polymorphism) genotyping data supported the two-species hypothesis (De Castro *et al.*, 2013).

Adding to the debate, nuclear and chloroplast DNA provided evidence of differentiation between populations of *Platanus mexicana* var. *mexicana* from the Balsas Basin in central Mexico and those in Veracruz and Chiapas (Feng *et al.*, 2005). This raises various questions: How important is physiographic diversity for the differentiation of *P. mexicana* var. *mexicana* populations with high hybridization potential? Can the Balsas Basin be considered a climate refugium for this species? Is it possible to differentiate populations in Veracruz and Chiapas from those in Oaxaca (Balsas Basin) using highly polymorphic multiloci molecular markers such as ISSR (Inter Simple Sequence Repeat)? To answer these questions, a population genetics study was conducted on three *P. mexicana* var. *mexicana* populations from southern Mexico.

2. MATERIAL AND METHODS

2.1. Plant material

Leaves of *Platanus mexicana* var. *mexicana* (Mexican sycamore) were collected without mechanical damage from 30 randomly selected individuals in each of three wild riparian populations, maintaining a minimum distance of 25 m between sampled trees to ensure genetic independence. The plant material was dried following the procedure suggested by Chase & Hills (1991), and stored until analysis. The sampled populations were located in tropical cloud forests in Ixtapa, Chiapas (1234 m asl; 16° 47' 17" N; 95° 50' 53" W) and San Juan Comaltepec, Oaxaca (900 m asl; 17° 19' 19" N; 95° 59' 5" W), as well as in a transition zone between tropical cloud forests and lowland forests in Colipa, Veracruz (620 m asl; 16° 49' 24" N; 96° 47' 43" W) (Fig. 1). The studied populations were located 387 ± 124 km from each other and were considered independent as the distance of *Platanus* pollen flux is 2.7 km (Bricchi *et al.*, 2000). Low genetic structure among riparian *P. mexicana* populations along a 1700-m elevation gradient in Veracruz has been explained by transport of pollen and seeds (Galván-Hernández *et al.*, 2015). A small number of migrants is sufficient to alter the genetic structure of the dominant population through genetic drift (Grueva & Zhelev, 2011).

2.2. DNA extraction and ISSR amplification.

DNA extraction was performed following the method of Doyle & Doyle (1990) with minor modifications. DNA quantity and quality were determined by spectrophotometry at 260 nm and gel electrophoresis. Ten ISSR UBC (University of British Columbia) primers were selected (Table 1) based on a clear and reproducible banding pattern. ISSR markers were used due to their capacity to evaluate differentiation between and within populations, to estimate homozygotes and

heterozygotes, as well as to identify alleles associated with different evolutionary forces exclusive of each population (Bornet & Branchard, 2001; Foll & Gaggiotti, 2008; Trieu et al., 2016; Wang et al., 2017).

Amplification was performed following the procedure described by Xiao & Gong (2006) with slight modifications. The total volume of the PCR reaction was 20 μ L with 10 ng of template, 1x (NH₄)₂SO₄ buffer, 3 mM MgCl₂, 0.375 mM dNTPs, 1 μ M of each primer, 1 unit of Taq DNA polymerase (Fermentas) and double distilled water. The thermal cycle was as follows: initial denaturation at 94 °C for 4 minutes, followed by 35 cycles of 30 seconds at 94 °C, 45 seconds at the annealing temperature of each primer (50 °C for 818, 824, 827, 829; 53 °C for 835, 841, 845, 848, 850 and 857), and 90 seconds at 72 °C; followed by a final extension at 72 °C for 8 minutes. Amplification products were separated by gel electrophoresis and documented using the Kodak ID 3.5 image analysis software.

Table 1. Primers for the ten ISSR UBC genetic markers selected for this study.

Tabla 1. Iniciadores para los diez marcadores genéticos ISSR UBC seleccionados para este estudio.

Primer	Sequence	Size Range (base pairs)	Bands	Polymorphic bands
818	(CA)8G	350-1000	12	9
824	(TC)8G	350-1500	9	8
827	(AC)8G	400-1400	9	8
829	(TG)8C	480-1700	7	4
835	(AG)8YC	180-1400	9	7
841	(GA)8YC	300-1200	9	7
845	(CT)8RG	250-1500	12	10
848	(CA)8RG	300-1500	10	9
850	(GT)8TYC	300-1500	13	11
857	(AC)8YG	180-1500	15	14
Total Bands			105	87

Y: pyrimidine; R: purine.
Y: pirimidina; R: purina

2.3. Data analysis

The amplified bands were recorded as 1 (present), 2 (absent) or 0 (non-amplified). Percentage of polymorphic loci (% P), number of alleles per locus (A), effective number of alleles per locus (Ne), expected heterozygosity (He) and Shannon index (I) were estimated from the allele frequencies p and q with the adjustment of Lynch & Milligan (1994) using TFPGA v. 1.3 (Miller, 1997). An AMOVA was performed with GenAlEx v. 6.41 (Peakall & Smouse, 2006) to determine the partition of genetic variation within and between populations. Genetic distance was estimated using the method of Nei & Lee (1979) and a UPGMA dendrogram was made using TFPGA v. 1.3.

Outliers in allele frequencies possibly associated with processes of natural selection were identified using BayeScan v.1.0 (Foll & Gaggiotti, 2008). The model was iterated 5,000 times with 20-iteration intervals between samples. The log₁₀ of the

Bayesian Factor (BF) was considered with substantial ($p = 76$) and strong ($p = 90.9$) cuts on Jeffreys' scale of evidence. BF is the probability that an allele frequency at a specific locus corresponds to an M1 or M2 model (neutral or under selection, respectively); high BF values indicate that the M2 model better fits the data. Jeffreys' criterion is the percentage of iterations in which an allele shifts away from the neutral model (M1).

An additive model with the option of correlated allele frequencies between populations (Falush *et al.*, 2007) was used in the STRUCTURE software to assess the genetic structure of populations. A total of 50,000 MCMC (Markov Chain Monte Carlo) iterations were realized for both elements and 50 runs for each K were evaluated ($K = 1$ to $K = 10$). The estimated value of stock (K) was determined by the graphical method ΔK proposed by Evanno *et al.* (2005). Finally, gene flow between populations was calculated from the coefficient of genetic differentiation (F_{ST}) with the formula $Nm = (1 - F_{ST}) / 4F_{ST}$ (Slatkin & Barton, 1989), where Nm is the number of migrants per generation.

3. RESULTS

A total of 131 loci were identified on 81 individuals using the ISSR markers; 29 from Chiapas, 23 from Oaxaca and 29 from Veracruz. All genetic variability indices had higher values for Oaxaca compared with Chiapas and Veracruz (Table 2).

Table 2. Genetic variability indices of *P. mexicana* var. *mexicana* populations in southern Mexico.

Tabla 2. Índices de variabilidad genética entre poblaciones de *P. mexicana* var. *mexicana* en el sur de México.

Population	N	A	Ne	He	P	I
Chiapas	29	1.649	1.365	0.225	67.176	0.340
Oaxaca	23	1.832	1.408	0.250	68.702	0.379
Veracruz	29	1.588	1.385	0.234	65.649	0.353

N: individuals estimated by TFPGA v. 1.3; A: alleles per locus; Ne: effective number of alleles per locus; He: expected heterozygosity; P: polymorphism; I: Shannon index

N: Individuos estimados por TFPGA v. 1.3; A: Alelos por locus; Ne: Número de alelos por locus; He: heterocigotos esperados; P: polimorfismo; I: Índice de Shannon

The AMOVA revealed a significant genetic structure ($F_{ST} = 0.235$, $p < 0.001$), with three times more variation within than among populations (Table 3). The Oaxaca and Veracruz populations were genetically more similar (Fig. 2), significantly different from the Chiapas population as shown by the genetic distance value (Nei = 0.134).

Table 3. AMOVA of *P. mexicana* var. *mexicana* populations in Oaxaca, Veracruz and Chiapas.

Tabla 3. AMOVA para poblaciones de *P. mexicana* var. *mexicana* en Oaxaca, Veracruz y Chiapas.

Source	df	SS	MS	F	%
Among populations	2	349.571	174.785	5.571	24
Within populations	82	1433.747	17.485	17.485	76
Total	84	1783.318		23.056	100

df: degrees of freedom; SS: sum of squares; MS: mean squares; F: Fisher's estimate; %: percentage of accumulated variance.

df: grados de libertad; SS: suma de cuadrados; MS: cuadrados medios; F: Estimados de Fisher; %: Porcentaje de variación acumulada

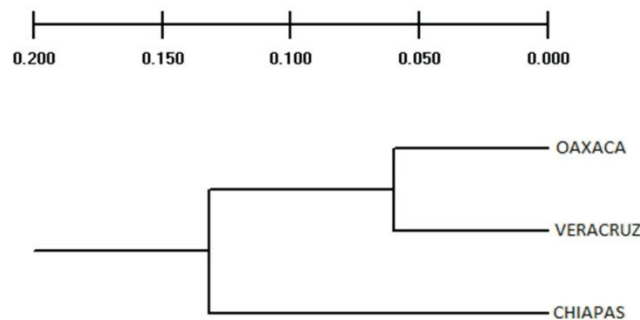


Fig. 2. UPGMA dendrogram based on Nei's genetic distance between *P. mexicana* var. *mexicana* populations in Oaxaca, Veracruz and Chiapas.

Fig. 2. Dendrograma UPGMA basado en las distancias genéticas de Nei entre poblaciones de *P. mexicana* var. *mexicana* en Oaxaca, Veracruz y Chiapas.

The outlier analysis showed that ten loci exceeded Jeffreys' substantial criterion and six loci exceeded the strong criterion (Fig. 3), hence subject to the effects of natural selection. The latter six loci were less frequent in Veracruz (0.11 ± 0.13), followed by Oaxaca (0.50 ± 0.42) and Chiapas (0.70 ± 0.35). The allelic frequencies showed higher genetic difference between populations when considering those 6 loci ($F_{ST} = 0.376 \pm 0.05$) (Table 4), compared to the general differentiation ($F_{ST} = 0.235$, $p < 0.001$). Differentiation was lower between the Oaxaca and Veracruz populations, indicating higher gene flow (Table 5).

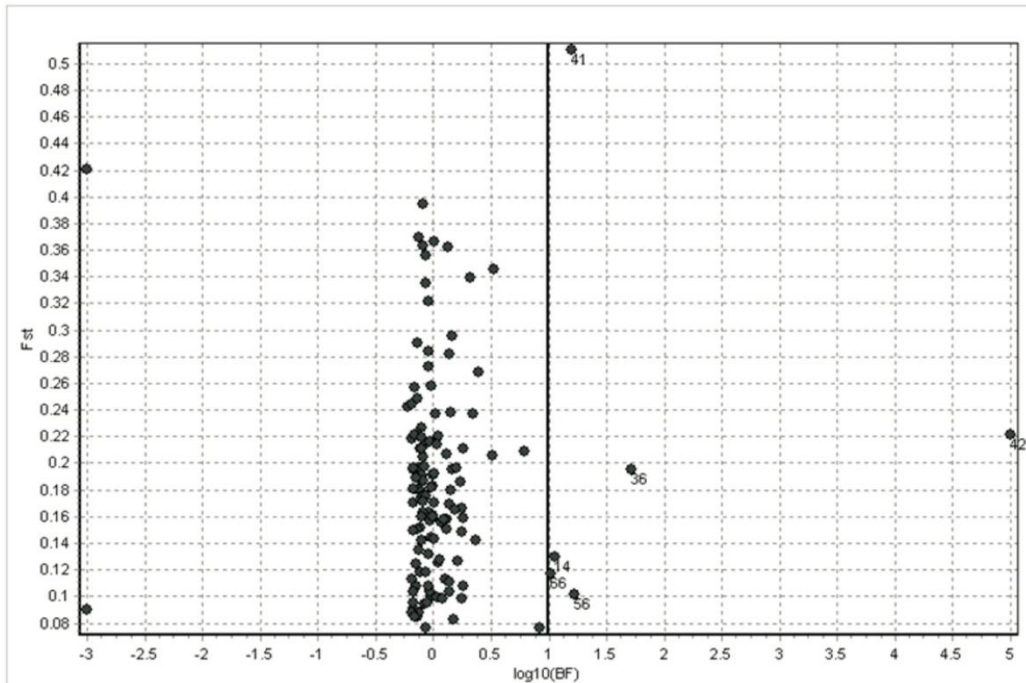


Fig. 3. Bayesian analysis of allelic frequencies for *P. mexicana* var. *mexicana* populations in southern Mexico. Six loci shifted away from the expected allelic frequencies under a model of natural selection. The cut line corresponds to Jeffreys' strong criterion.

Fig. 3. Análisis Bayesiano de frecuencias alélicas para población de *P. mexicana* var. *mexicana* en el sur de México. Seis loci se alejan de las frecuencias alélicas esperadas bajo el modelo de selección natural. La línea de corte corresponde al criterio de Jeffreys.

Heterozygosity and the Shannon index were higher in Chiapas for the six loci exceeding Jeffreys' strong criterion ($H_e = 0.365$; $I = 0.525$) than for all loci combined ($H_e = 0.225$; $I = 0.340$), suggesting that selection favored heterozygotes for these loci in Chiapas. To the contrary, the values were lower in Oaxaca when considering only those six loci ($H_e = 0.231$; $I = 0.369$) compared to global values ($H_e = 0.250$; $I = 0.379$). The same situation was found in Veracruz ($H_e = 0.205$ and $I = 0.310$ for the six loci, compared to $H_e = 0.234$ and $I = 0.353$ globally).

The STRUCTURE analysis showed that the best explanation for population structure was found with $K = 3$, hence identifying three groups corresponding to each population. The Oaxaca and Veracruz populations shared allelic variables, and were different from the Chiapas population (Fig. 4). Gene flow was higher between Oaxaca and Veracruz ($N_m = 1.50$) (Table 5), in line with the results from the UPGMA (Fig. 2).

Table 4. Populations' allelic frequencies for the loci shifting away from the neutral natural selection model obtained on the Bayesian analysis.

Tabla 4. Frecuencias alélicas de las poblaciones para los loci que se alejan del modelo de selección neutral obtenido en el análisis Bayesiano.

Loci	Population	FA	p	Log₁₀BF	α	F_{ST}	Jeffreys
	Chiapas	0.9					
12	Oaxaca	0	0.91878	1.0536	1.1624	0.36874	90.9
	Veracruz	0.2333					
	Chiapas	0.8666					
34	Oaxaca	1	0.98100	1.7128	1.2741	0.39171	90.9
	Veracruz	0.1333					
	Chiapas	0.7179					
39	Oaxaca	1	0.93979	1.1933	1.1563	0.36662	90.9
	Veracruz	0.2333					
	Chiapas	0.8666					
40	Oaxaca	1	1.0000	1000.0	1.8125	0.51110	90.9
	Veracruz	0					
	Chiapas	1					
54	Oaxaca	0.32	0.94379	1.2251	1.1701	0.36898	90.9
	Veracruz	0.1666					
	Chiapas	0.1333					
64	Oaxaca	0.76	0.91298	1.0209	1.1434	0.36385	90.9
	Veracruz	0					
	Chiapas	0.7666					
57	Oaxaca	0.04	0.76875	0.52171	0.99755	0.33520	76
	Veracruz	0					
	Chiapas	1					
58	Oaxaca	0.32	0.86177	0.79480	1.0658	0.34687	76
	Veracruz	0.3666					
	Chiapas	0					
112	Oaxaca	0.6	0.89178	0.91594	1.1287	0.36153	76
	Veracruz	0					
	Chiapas	0.7					
117	Oaxaca	0	0.76335	0.50862	1.0292	0.34260	76
	Veracruz	0					

FA: allelic frequencies, F_{ST}: fixation index.

FA: Frecuencia alélica ; F_{ST}: índice de fijación

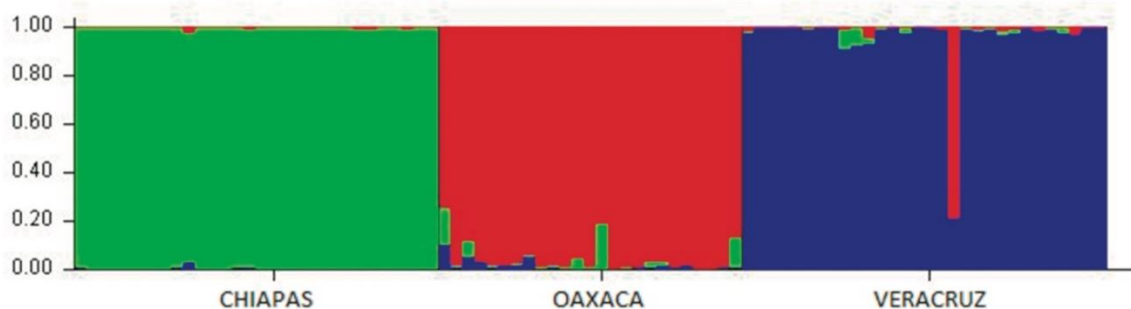


Fig. 4. STRUCTURE analysis ($K = 3$) showing the proportion of shared genetic groups among three populations of *P. mexicana* var. *mexicana*.

Fig. 4. Análisis de STRUCTURE ($K = 3$) que muestra la proporción de grupos genéticos compartidos entre tres poblaciones de *P. mexicana* var. *mexicana*.

Table 5. Gene flow estimate between populations of *P. mexicana* var. *mexicana* in southern Mexico.

Tabla 5. Flujo genético estimado entre poblaciones de *P. mexicana* var. *mexicana* en el sur de México.

Comparison	F_{ST}	Nm
Chiapas-Oaxaca	0.2733	0.6647
Chiapas-Veracruz	0.2901	0.6118
Oaxaca-Veracruz	0.1427	1.5019

F_{ST} : fixation index; Nm: migrants per generation.

F_{ST} : índice de fijación; Nm: migrantes por generación.

4. DISCUSSION

The *Platanus mexicana* var. *mexicana* population located in Oaxaca had a higher genetic diversity than the other two studied populations, strengthening the assertion that the Balsas Basin might be a climate refugium (Luna-Vega, 2008). Relict populations generally have higher levels of genetic diversity than rare or endemic populations (e.g., Konnert & Bergman, 1995; Demesure *et al.*, 1996; Soltis *et al.*, 1997; Sinclair *et al.*, 1998; Esselman *et al.*, 2000). Higher gene flow was noted between the Oaxaca and Veracruz populations, possibly explained by higher topographic connectivity compared with the Chiapas population. This suggests that the area between the Oaxaca and Veracruz populations could be an intraspecific hybridization zone. However, heterozygosity and percentage of polymorphic loci were lower in Veracruz than Oaxaca, indicating differentiation despite the hybridization potential. It has been suggested previously that different genotypes can exist in adjacent continental regions (Hewitt, 2011). Hence, despite topographic connectivity, allopatric processes seem to be at play between the Oaxaca and Veracruz populations. Indeed, the STRUCTURE analysis showed that while both populations shared some alleles, most were exclusive.

Allopatric differentiation processes can occur due to selective pressure increasing differentiation, whether or not there is gene flow between populations (Avice, 2004). The Bayesian model indicated important allele loss in the Veracruz region related with high environmental pressure. The weather in Veracruz ranges from warm to temperate and *P. mexicana* var. *mexicana* can grow there as low as 70 m asl, which is well outside the described range for this species. Therefore, even with a gene flow between 1.5 and 4.1 migrants per generation between the alleged Pleistocene refuge (Oaxaca) and allopatric population (Veracruz), migrant alleles are likely eliminated as they do not confer adaptive advantage. Further analysis with co-dominant genetic markers will be necessary to more accurately evaluate the effect of natural selection in the Veracruz region.

The Chiapas population presented greater genetic differentiation compared to the Oaxaca and Veracruz populations, but without significant differences in heterozygosity and polymorphism. The Sierra Norte de Oaxaca is a topographic barrier separating the Oaxaca and Veracruz populations (to the north-west) from the Chiapas population (to the south-east). In the state of Chiapas, there are only a few isolated patches of tropical cloud forest near Cerro Azul (CONABIO, 2010), and the *Platanus* population sampled at the Ixtapa site is surrounded by tropical vegetation. Geographical discontinuity might thus explain the higher genetic differentiation, but not the apparent allelic richness.

According to the Pleistocene refugia hypothesis, tropical cloud forests were relegated to a few areas at mid-altitude during glaciations (Toledo, 1982; Aide & Rivera, 1998; Vovides *et al.*, 2004), between too cold conditions at higher altitudes and too dry conditions at lower altitudes (Ramírez-Barahona & Eguiarte, 2013). Tropical cloud forests expanded again during interglacial periods, this cyclic pattern of contraction and expansion generating a reticulate genetic structure due to successive isolation and reconnection of populations (Comes & Kadereit, 1998; Edwards *et al.*, 2016). However, the Pleistocene refugia hypothesis has been contested, as some researchers could not find evidence of prolonged drought at low altitudes during glaciations (Colinvaux *et al.*, 2000; Willis & Whittaker, 2000), suggesting continued connectivity of tropical cloud forests (Ramírez-Barahona & Eguiarte, 2013).

Previous studies have reported a reticulate genetic structure in *Platanus* from northern Mexico, but substantial differentiation towards the south (Nixon & Poole, 2003; Feng *et al.*, 2005; Grimm & Denk, 2008). The results presented here support categorical separation without reticulate exchange between *Platanus* populations in Chiapas and Oaxaca, as there was little allelic connection between north and south (Veracruz-Chiapas) and west and east (Oaxaca-Chiapas). Moreover, if the Chiapas population had originated from postglacial expansion from a Oaxaca refugium, it would show a substantial loss of genetic variability, which is not the case. It is therefore suggested, in line with previous studies (Feng *et al.*, 2005; Luna-Vega, 2008), that genetic differentiation of the Chiapas *Platanus* population is due to a process of vicariance which could be explained by topographic heterogeneity, especially in the upper Grijalva Basin.

According to the results of the present study, the genetic structure of *Platanus mexicana* var. *mexicana* in southern Mexico can be explained by three processes: 1) Population contraction and expansion of a refugium in Oaxaca during the

Pleistocene, with allelic exchange towards the north; II) Allopatric differentiation towards the Gulf of Mexico (Veracruz) due to natural selection; III) Vicariance towards the south of the distribution, with substantial differentiation in Chiapas.

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

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