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Genetic diversity of *Fusarium oxysporum* associated to the banana Fusarium wilt

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ABSTRACT

Background/Objective. The research objective was to analyze *Fusarium oxysporum* (Fo) isolates from different banana regions from México using SSR markers.

Materials and Methods. Pseudostems of *Musa* plants exhibiting wilt-disease were sampled from 'Pisang Awak' (ABB), 'Silk' (AAB), and 'Bluggoe' (ABB) varieties collected on commercial orchards of five banana-producing areas of México: Colima, Michoacán, Jalisco, Nayarit, and Yucatán states. Six SSR loci were analyzed for population structure based on 96 *Fusarium oxysporum* isolates. The number and frequency of haplotypes were calculated in POPGENE. With this data, using the dissimilarity index of Morisita in the R package vegan, the genetic similarity of the populations was estimated. With the haplotype data, we also conducted a molecular analysis of variance (AMOVA) to evaluate the genetic differentiation between regions (FCT), among populations in each region (FSC), and among all populations included in the analysis (FST). Additionally, to illustrate the relations among haplotypes, and their distribution and frequency among sampled populations we generate a minimum spanning network.

Results. After seven days of PDA culture, all isolates had cottony white mycelia, which can be flat to aerial, and can be colored on the upper surfaces from light violet to dark violet. But on the bottom surfaces, the colony can have colorations from orange to dark red. We observed short monophialides, unicellular or bicellular with oval microconidia. Macroconidia were falciform, and with three to four septa. Putatively, these characteristics fit the *F. oxysporum* taxonomic criteria. All tested loci were polymorphic across the 96 Foc. We detect 16 haplotypes, of which the most frequent and common was the H16; the others were rare and could be widely dispersed or restricted to one or two populations. Also, we did not find genetic differences among the three analyzed populations, as well as we did not find genetic structure or differentiation at any level. These findings are related to Foc isolates as a complex not necessarily to those related to Foc races.

Conclusion. Our analyses did not detect significant genetic differences between the Fo populations studied, nor did we find genetic structure or differentiation at any level. Therefore, our data suggests that the analyzed populations constitute a single metapopulation, despite the presence of infrequent or unique haplotypes.

Keywords: Foc R4T, Banana genotypes, SSR markers

INTRODUCTION

Bananas and plantains (*Musa* spp.) are the fourth most important crop in the world, surpassed only by rice, wheat, and corn (FAOSTAT, 2024). This fruit is available throughout the year and is grown in 135 countries in the tropical and subtropical regions. Although banana represents a significant source of income in the Latin American region, only 15% of the production is exported as a commodity since most harvest is in small farms or backyards, for domestic consumption or local markets (FAOSTAT, 2024).

Bananas and plantains are affected by several pathogens worldwide, however, Fusarium wilt, which is caused by a complex of isolates of the fungus *Fusarium oxysporum* (Fo). The specific complex of *F. oxysporum* f. sp. *cubense* (Foc), constituted for at least four races, is considered the most destructive diseases for this crop (van Westerhoven *et al.,* 2022). Foc produces three types of asexual spores: macroconidia, microconidia, and chlamydospores, which have roles in dispersal, reproduction, and survival (Pegg *et al*., 2019). Once Foc invades a plantation, it is hard to control, because the pathogen persists in the soil for long periods (Maryani *et al*., 2019). Thus, the most effective alternative to control the disease is the replacement of susceptible cultivars with others resistant to the pathogen.

In the past, nearly all commercial plantations in the world changed their susceptible varieties by Cavendish subgroup genotypes (Genome AAA). The recent emergence of Foc Tropical race 4 (Foc R4T in Spanish), which is capable to infect members of the Cavendish subgroup, has become the main threat to the banana and plantains industry. This is more problematic because currently, the markets demand primarily fruits of the 'Giant Naine' clone from the Cavendish subgroup (Genome AAA), and there are no other resistant banana genotypes available (Ordoñez, 2018). In México, nearly forty thousand hectares of 'Gros Michel' cultivar was devastated in the mid-1950s due to Foc race 1, forcing its replacement by resistant clones of the 'Cavendish' subgroup, such as 'Grand Naine'. For example, a decade ago, the state of Nayarit had 3,000 ha of 'Silk' and 3,500 ha of 'Gros Michel' cultivars. Recently, banana and plantain production in México has been concentrated in 16 states, with Chiapas, Tabasco, Colima, and Veracruz state being the main producers, accounting for 72.5% of the planted area, 75.3% of the volume produced, and 66.3% of the value of the crop's production. The volume obtained in 2023 was 2,642,338 tons, 1.9% higher than the previous year's production (SIAP, 2024).

Knowledge of the genetic diversity of populations of phytopathogenic fungi and their mode of reproduction is relevant for crop management programs, and to reduce the impact of the disease (McDonald and Linde, 2002). In the case of Foc, it has a relatively diverse genetic structure for an asexual reproductive fungus (Martínez-de la Parte *et al*., 2024). The genetic information of the pathogen can be used to design effective management practices for the disease, as well as for breeding programs to develop a resistant or tolerant banana

cultivar, and for quarantine purposes in a particular country or geographical location (Magdama *et al*., 2020; van Westerhoven *et al.,* 2022; Chittarath *et al*., 2022; Baruah *et al*., 2025). In México, despite the sustained increase in the number of plantations of banana and plantain, information regarding the diversity and genetic structure of Foc is scarce. This reserach present the first analysis that studies Fo isolates from different regions using SSR markers as a preliminary approximation to justify deep Foc diversity studies.

Sampling was conducted directly on *Musa* plants from 'Pisang Awak' (ABB), 'Silk' (AAB), and 'Bluggoe' (ABB) varieties, affected by Fusarium wilt in five banana-producing areas of México: Colima, Michoacán, Jalisco, Nayarit, and Yucatán states. (Table 1). In each sampled plantation, we gather pseudostems of six- to eight-month-old wilting symptomatic plants. Discolored vascular strands were cut into 2–4 pieces and stored in a paper bag. In the laboratory, it was obtained single-spore cultures using the protocol proposed by Mostert *et al*. (2017). The morphology and cultural characteristics of Foc isolates were determined as described by Leslie and Summerell (2006). The isolates were stored in sterile glycerol 15% (v/v) at -80 °C. Further testing to verify the isolate identity to *F. oxysporum* f. sp. *cubense* was not conducted. For genomic DNA extraction of 96 monosporic Foc cultures, we followed the protocol of Möller and Bahnweg (1992). We analyzed six SSR loci for haplotypes characterization. The primers used are listed in Table 2. Because these SSR were suggested to study the structure of *F. oxysporum* (Fo) (Bogale *et al*., 2005), it is assumed that this work targeted isolates of Fo as well as those belonging to Foc races but race 4 (Foc R4T), which is officially not reported in Mexico. PCR cycles were done as specified by Bogale *et al*. (2005). The PCR products were analyzed by electrophoresis in 1.5% agarose gel and then stained in ethidium bromide solution and documented in a ChemiBis MF-2 system (Bio-Imaging Systems, Neve Yamin, Israel). A binary matrix for the six loci and a total of 96 isolates was constructed.

Table 1. Sampling for *F. oxysporum* from banana commercial orchards at five Mexican states.

Isolate	County	State	Cultivar	Geographic location	Altitude (msnm)
ACM1	Armería	Colima	Silk (AAB)	18°53′23"N, 104° 0′ 0" O	11
ACM2			Silk (AAB)	18°53′23"N, 104° 0′ 0" O	11
ACP1			Bluggoe (ABB)	18° 54′ 52"N, 103° 59′38" O	11
ACP2			Bluggoe (ABB)	18° 54′ 52"N, 103° 59′38" O	11
ACM3			Silk (AAB)	18°54′5"N, 103°54′31"O	11
ACM4			Silk (AAB)	18°54′5"N, 103°54′31"O	11
ACM10			Silk (AAB)	18°53′10"N, 103°59′37"O	11
ACP11			Bluggoe (ABB)	18°55′24"N, 103°57′49"O	11
ACP15			Bluggoe (ABB)	18°55′24"N, 103°57′49"O	11
ACM13			Silk (AAB)	18°55′34"N, 103°58′2"O	11
TCM1	Tecomán	Colima	Silk (AAB)	18°55′3"N, 103°5′ 13′′O	40
TCM2				18°55′3"N, 103°5′ 13′′O	40
TCM8				18°48′44"N, 103°42′49" O	69
TCM9				18°48′44"N, 103°42′49" O	69
TCM10				18°48′44"N, 103°42′49" O	69
TCM11				18°48′44"N, 103°42′49" O	69
TCM12				18°48′44"N, 103°42′49" O	69

TCM13				18°50′ 54′′N, 163°99′ 28′′ O	27
TCM14				18°50′ 54′′N, 163°99′ 28′′ O	27
TCM15				18°50′ 54′′N, 163°99′ 28′′ O	27
TCM16				18°50′ 54′′N, 163°99′ 28′′ O	27
TCM1				18°58′2”N, 103° 50′33” O	62
MCP1	Manzanillo	Colima	Bluggoe (ABB)	18°57′0”N, 104°3′40”O	22
MCT3			Pisang awak (ABB)	109°02′48”N, 104°06′35”O	70
MCT4			Pisang awak (ABB)	109°02′48”N, 104°06′35”O	70
MCT5			Pisang awak (ABB)	109°02′48”N, 104°06′35”O	70
MCT6			Pisang awak (ABB)	109°02′48”N, 104°06′35”O	70
MCM7			Silk (AAB)	109°0′52”N, 104°9′22”O	21
MCM9			Silk (AAB)	109°0′52”N, 104°9′22”O	21
MCM10			Silk (AAB)	109°0′52”N, 104°9′22”O	21
MCM11			Silk (AAB)	109°0′52”N, 104°9′22”O	21
MCM13			Silk (AAB)	19°00′46”O, 104°09′25”O	21
MCM14			Silk (AAB)	19°00′46”O, 104°09′25”O	21
MCM15			Silk (AAB)	19°02′21”N, 104°14′08”O	16
SNM1	San Blas	Nayarit	Silk (AAB)	21°32′25”N, 105°07′51”O	325
SNP1			Bluggoe (ABB)	21°32′32”N, 105°08′01”O	206
SNM2			Silk (AAB)	21°32′32”N, 105°08′05”O	206
SNM3			Silk (AAB)	21°32′32”N, 105°08′05”O	206
SNM4			Silk (AAB)	21°32′41”N, 105°08′05”O	206
SNM5			Silk (AAB)	21°32′44”N, 105°08′12”O	206
SNM5.2			Silk (AAB)	21°32′44”N, 105°08′12”O	206
SNM6			Silk (AAB)	21°32′44”N, 105°08′12”O	206
SNM7			Silk (AAB)	21°32′44”N, 105°08′12”O	206
SNM8			Silk (AAB)	21°32′44”N, 105°08′17”O	206
SNM9			Silk (AAB)	21°32′44”N, 105°08′17”O	206
SNM10			Pisang awak (ABB)	21°26′36”N, 105°11′20”O	33
SNT1			Pisang awak (ABB)	21°26′36”N, 105°11′20”O	33
SNT2			Pisang awak (ABB)	21°26′36”N, 105°11′20”O	33
SNT3			Pisang awak (ABB)	21°26′36”N, 105°11′20”O	33
SNT4			Pisang awak (ABB)	21°26′36”N, 105°11′20”O	33
SNT5			Pisang awak (ABB)	21°26′36”N, 105°11′20”O	33
SNT6			Pisang awak (ABB)	21°26′36”N, 105°11′20”O	33
AYP1	Akil	Yucatán	Bluggoe (ABB)	20°15′53”N, 89°21′37”O	32
AYP2			Bluggoe (ABB)	20°5′55”N, 89°21′37”O	32
AYM1			Silk (AAB)	20°15′52”N, 89°2′37”O	32
AYM2			Silk (AAB)	20°15′52”N, 89°21′22”O	32
OYM4	Oxkutzcab	Yucatán	Silk (AAB)	20°13′38”N, 89°27′32”O	49
OYM5			Silk (AAB)	20°13′38”N, 89°27′32”O	49
OYM6			Silk (AAB)	20°13′14”N, 89°26′30”O	49
OYM7			Silk (AAB)	20°13′38”N, 89°27′32”O	49

OYM8			Silk (AAB)	20°13′38”N, 89°27′32”O	49
OYM9			Silk (AAB)	20°13′38”N, 89°27′32”O	49
OYP3			Bluggoe (ABB)	20°13′38”N, 89°27′32”O	49
OYM10			Silk (AAB)	20°16′42”N, 89°22′52”O	32
OYM11			Silk (AAB)	20°16′42”N, 89°22′52”O	32
OYM12			Silk (AAB)	20°16′42”N, 89°22′52”O	32
OYM13			Silk (AAB)	20°16′42”N, 89°22′52”O	32
OYM14			Silk (AAB)	20°16′42”N, 89°22′52”O	32
CMM1				18°40′41”N, 103°40′29”O	21
CMM2				18°40′43”N, 103°40′31”O	21
CMM3				18°40′22”N, 103°41′22”O	29
CMM4				18°39′57”N, 103°41′27”O	29
CMM5	Coahuayana	Michoacán	Silk (AAB)	18°44′04”N, 103°40′01”O	27
CMM6				18°44′04”N, 103°40′01”O	27
CMM7				18°42′59”N, 103°42′03”O	27
CMM8				18°42′59”N, 103°42′03”O	27
CMM9				18°42′59”N, 103°42′03”O	27
RJP1			Silk (AAB)	19°10′30.42′′N 104°36′01.13′′O	12
RJP2			Silk (AAB)	19°10′30.22′′N, 104°36′01.25′′O	12
RJP3			Silk (AAB)	19°10′30.22′′N, 104°36′01.57′′O	12
RJP4			Silk (AAB)	19°10′30.04′′N, 104°36′01.74′′O	12
RJP5			Silk (AAB)	19°10′29.93′′N, 104°36′02.17′′O	12
RJP6			Silk (AAB)	19°10′29.83′′N 104°36′02.41′′O	12
RJP7			Silk (AAB)	19°10′39.42′′N 104°36′07.12′′O	12
RJP8			Silk (AAB)	19°10′38.67′′N 104°36′06.60′′O	12
RJP9			Silk (AAB)	19°10′38.38′′N 104°36′05.71′′O	12
RJP10	El Rebalse	Jalisco	Silk (AAB)	19°10′38.86′′N 104°36′07.77′′O	12
RJP11			Bluggoe (ABB)	19°10′38.66′′N 104°36′06.80′′O	14
RJM12			Bluggoe (ABB)	19°10′39.20′′N 104°36′09.30′′O	14
RJM13			Bluggoe (ABB)	19°10′38.68′′N 104°36′09.20′′O	14
RJM14			Bluggoe (ABB)	19°11′15.86′′N, 104°35′29.56′′O	14
RJM15			Bluggoe (ABB)	19°11′16.26′′N, 104°35′29.50′′O	14
RJM16			Bluggoe (ABB)	19°11′17.05′′N, 104°35′17.05′′O	14
RJM17			Bluggoe (ABB)	19°11′17.35′′N, 104°35′27.92′′O	14
RJM18			Bluggoe (ABB)	19°11′17.72′′N, 104°35′26.70′′O	14
RJM19			Bluggoe (ABB)	19°11′21.94′′N, 104°35′09.52′′O	14
RJM20			Bluggoe (ABB)	19°11′21.83′′N, 104°35′08.53′′O	14

Table 2. Simple sequence repeat (SSR) primers used to analyze *Fusarium oxysporum* isolates genetic diversity (modified from Bogale *et al*., 2005).

Primer	[x] Primer secuence (5´-3´)		Annealing temperature (°C)
G1/ MV15	F:	CTCGTCCTTTGCGAATGACC	58
	R:	GACCACCTCGGTGATGGTGAGACGG	
	R:	CAAGCCGCTCTCCACGGCGAAGGCG	
MB18	F:	GGTAGGAAATGACGAAGCTGAC	57
	R:	TGAGCACTCTAGCACTCCAAAC	
	R:	CGTCCTCAAGAGCAGCGAC	

[x] *F: forward R: reverse*

The total isolates were organized into three groups, to improve the robustness of the analysis and to facilitate data interpretation. Thus, we considered isolates form Colima, Jalisco and Michoacán as a single population because of their regional continuity and the lack of apparent ecological barriers. Isolates from Nayarit integrate the second population, and those from Yucatán are the third population. Later, based on geographical proximity and the banana fruit and propagule trading routes, these were further allocated into two regions: (i) East México (samples from Yucatán), and (ii) West México (isolates from Nayarit, Colima, Jalisco, and Michoacán). The number and frequency of haplotypes were calculated in POPGENE. With this data, using the dissimilarity index of Morisita in the R package vegan (Oksanen *et al*. 2019), the genetic similarity of the populations was estimated. With the haplotype data, we also conducted a molecular analysis of variance (AMOVA) to evaluate the genetic differentiation between regions (FCT), among populations in each region (FSC), and among all populations included in the analysis (FST). We performed the AMOVA in ARLEQUIN v. 3.5 using 1000 permutations. Additionally, to illustrate the relations among haplotypes, and their distribution and frequency among populations we generate a minimum spanning network. Genetic structure was inferred using the principal component analysis and the sparse non-negative matrix factorization (sNMF) in LEA (Frichot and François, 2015). We selected the preferred number of K using a cross-entropy criterion based on the prediction of masked genotypes to evaluate the error of ancestry estimation.

Results of cultural characterization showed that colony size development ranged from 8.7 to 9.8 mm per day on PDA medium at 28 °C. After seven days of culture, all isolates had cottony white mycelia, which can be flat to aerial, circular or irregular in shape, colored on the upper surfaces from light violet to dark violet. On the petri dish reverse, color colonies ranged from orange to dark red. Short monophialides had an average of 3–5 septa, unicellular or bicellular, with oval microconidia of 5–15 × 2.5–3.5 µm. Macroconidia were 23.5–47.8 × 3.3–4.8 µm, falciform, with three to four septa (Leslie and Summerell, 2006). These characteristics were typical to *Fusarium oxysporum*. All tested loci were polymorphic across the 96 Mexican isolates of *Fusarium oxysporum*. We detect 16 haplotypes, of which the most frequent and common was the H16 (Figure 1). The rest were widely dispersed or restricted to one or two populations.

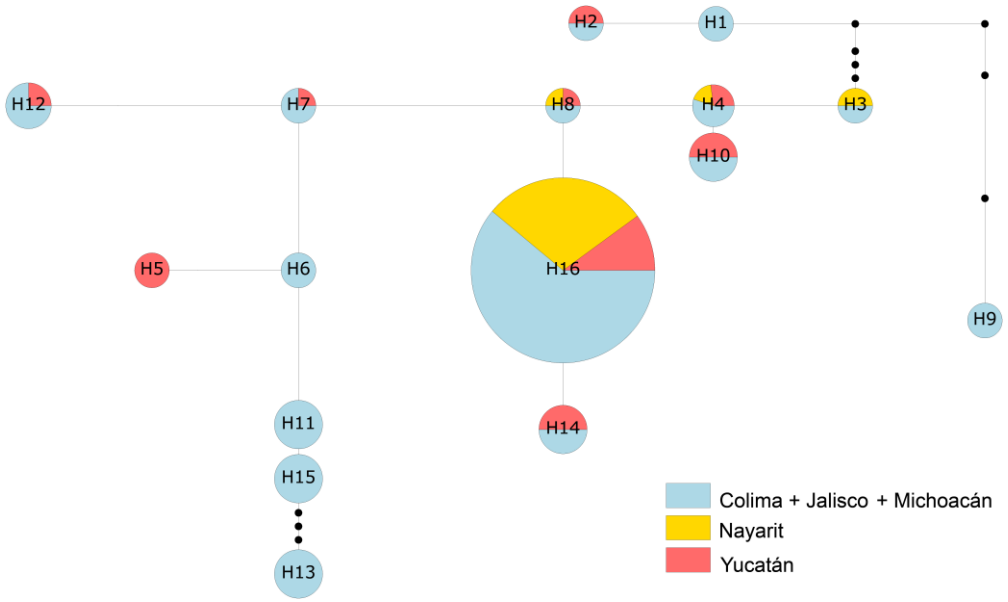

Figure 1. A minimum spanning network of 16 haplotypes found in the studied populations of *Fusarium oxysporum*. Small black dots along branches represent missing haplotypes. H withing circles is the ID haplotype, color denote population type, and circle size represents the haplotype frequency.

Genetic differences among the three analyzed populations were not significative (Table 3, Figure 2), nor at any comparison level (Table 4).

Table 3. Dissimilarity among sampled populations of *Fusarium oxysporum*.

Population	Colima, Jalisco and Michoacán	Nayarit	Yucatán
Colima, Jalisco and Michoacán	–	–	–
Nayarit	0.097	–	–
Yucatán	0.000	0.255	–

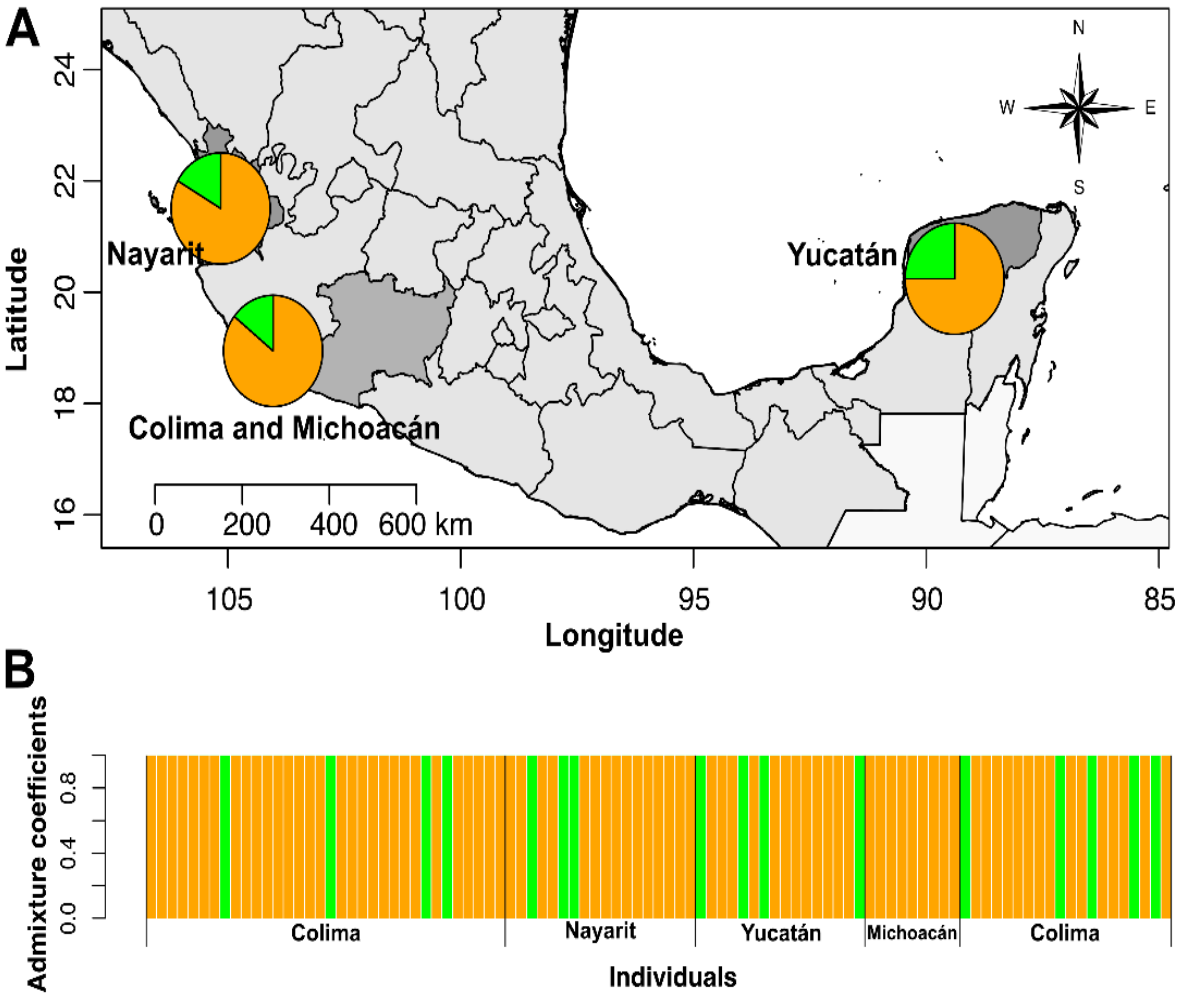

Figure 2. Genetic structure analysis of *Fusarium oxysporum* isolates from different locations based on sparse nonnegative matrix factorization (sNMF). (A) Population structure for K = 2 plotted on the map using the average ancestry coefficient values for each estimated population. (B) Group assignment probability of each sampled individual.

Table 4. Analysis of molecular variance (AMOVA) based on haplotypes associated to 96 isolates of *Fusarium oxysporum* from Colima, Jalisco, Michoacán, Nayarit and Yucatán state grouped into two regions (East and West México).

Source of variation[x]	d.f.	Sum of squares	Variance components	Variation (%)	*FI*	*P*
Between regions	1	0.921	-0.00145	-0.19	-0.00188	0.66960 ± 0.019
Between population within regions	1	1.012	0.00888	1.15	0.01150	0.21114 ± 0.014
Within populations	94	71.778	0.76359	99.04	0.00964	0.23460 ± 0.011
Total	96	73.711	0.77103	–	–	–

[x]*d.f., degrees of freedom; FI, fixation index; P, significance.*

According to these results, Mexican Fo populations are genetically similar (Tables 3 y 4). Magdama *et al*., (2020), also concluded that the populations of Foc in Ecuador comprise a single clonal lineage. In this work several Fo haplotypes were detected but only one was dominant (Figure 1). This may be related to the low variability rate of Fo as asexual organism compared to sexually reproducing organisms such as *Pseudocercospora fijiensis* (Manzo-Sánchez *et al*., 2019; McDonald and Linde, 2002). These results also agree with Bentley (1998), who detects only one Foc lineage in Mexican populations (lineage VIII). The same author describes that this lineage is unique in Central America, but he did not assign a vegetative compatibility groups (VCG) code. Ordoñez (2018) specifies that VCG 0124 found in México corresponds to the 0124/5/8/20 compatibility group complex, whose worldwide members had been identified withing the 1, 2, and 4 race. The Foc VCG found in México allows us to hypothesize that the pathogen in this country is a mixture between a native and introduced strains. If this is true, human activities are responsible for the dissemination of the clonal lineage.

The fungus *Fusarium oxysporum* f. sp. *cubense* is a genetically diverse pathogen with a cosmopolitan distribution. It is composed of four races, of which three infect plantains and bananas (Ploetz, 2015; Pegg *et al.,* 2019; Martinez-de la Parte *et al.*, 2024; Baruah *et al.,* 2025). Also, more than 24 vegetative compatibility groups have been recognized (Koening *et al*., 1997; Ordoñez, 2018; Maryani *et al*., 2019), and at least nine lineages phylogenetically clustered in two clades have been detected (Bentley *et al*., 1998; Czislowski *et al*., 2018; O'Donnell *et al*., 1998; Pegg *et al*., 2019). Because Foc reproduces preferentially asexually, its genetic diversity is grouped in clonal lineages (Bentley *et al*., 1998; Pegg *et al.,* 2019); this diversity can be enriched occasionally by parasexual events in which horizontal gene transfer can occur (Czislowski *et al*., 2018; Fourie *et al*., 2009; Ma *et al*., 2010; Vlaardingerbroek *et al*., 2016). Thus, the genetic structure of Foc (or the absence of it) corresponds to what is expected for an organism that preferentially reproduces asexually (McDonald and Linde, 2002). In fact, the genetic diversity of this pathogen (most VCG) is concentrated in its center of origin, and only a few VCG are scattered around the world (Bentley *et al*., 1998; Koening *et al*., 1997; Mostert *et al*., 2017), which can explain the absence of detectable genetic structure in the sampled populations.

Why Foc is diverse, and cosmopolitan worldwide, but locally may lack genetic structure? We found three possible explanations: one is that the pathogen had effectively spread because of the exchange of contaminated materials (rhizomes or leaf trash) (Ploetz, 2015). Another explanation is that it is a polyphyletic complex; thus, it is possible that native local strains parasitically converged to the introduction of *Musa* spp. (Gurr, 2011). The third possibility is that indeed *Musa* spp. may have dispersed together with some of the Foc clonal lineages which exchanged genetic information using parasexual or perhaps sexual mechanisms with local native linages (Ordoñez, 2018). In México it is not known the dispersal dynamics of Foc (Ordoñez, 2018), although Foc —mainly race 1— it is widely distributed in the territory.

In conclusion, cultural morphology of monosporic Foc isolates were consistent with what has been reported in the literature for Foc. Despite the haplotypes diversity found (16), H16 was the most frequent, while the remaining haplotypes may be either widely distributed or local, but with low frequency. No significant genetic differences were found among the studied populations or grouped by regions. Therefore, these results using six SSR markers suggest that the analyzed populations constitute a single metapopulation.

Conflicts interest

All the authors declare no conflict of interest.

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Author contributions

First, second and four authors provided the genomic methodology and sampling. Second author extensive sampling and phytosanitary problem conception. All contributed to writing and discussion.

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