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Essay

Papaya genetic resources in Mexico and their conservation for genetic improvement

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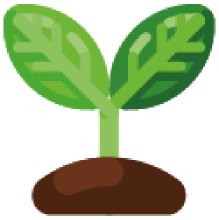
Abstract

Papaya (*Carica papaya* L.) is one of the fruit crops with the highest demand worldwide due to its pleasant flavor and multiple pharmacological properties. In Mexico, its cultivation and consumption are rooted in the population and have economic, social, and cultural importance. Mesoamerica is considered to be the center of origin and domestication, a place where a wide genetic diversity is found, which has been little studied and valued. Knowledge about genetic resources is essential to propose strategies of conservation and exploitation in the development of improved varieties since they are a source of genes for resistance to diseases, fruit quality, tolerance to abiotic factors, and rootstocks. Therefore, this work aimed to explore the existing information on the genetic resources of papaya (*Carica papaya* L.) in Mexico in terms of its conservation, biological collections, and the potential of outstanding traits to be incorporated into genetic improvement programs. To this end, a review was carried out on characterization, genetic diversity, and conservation status studies of wild, native, and domesticated relatives of papaya conducted in Mexico. There is valuable information on the variation, conservation, and evolutionary dynamics of papaya genetic resources in Mexico; however, there is insufficient information on the potential of genetic resources for use in genetic improvement. The unstudied and undocumented variation has a high risk of genetic erosion and extinction.

Keywords:

Carica papaya L., biological collections, genetic diversity, wild relatives.



Introduction

Plant breeding has impacted agronomy and food production since the early twentieth century and will continue to play a vital role in global food security (Tester and Langridge, 2010). Nonetheless, it is currently facing global challenges that affect productivity, accessibility, and nutritional quality, which is why it is necessary to use genetic resources for better performance in the development of new varieties (Swarup *et al*., 2021).

Successful crop breeding lies in efficiently identifying and incorporating genetic diversity from different sources, including commercial varieties, local varieties, wild and native species related to the crop of interest. Genetic diversity is described as the range of genotypic characteristics within a crop or species, while genetic variation refers to heritable differences between individuals for a specific trait where the contrasts reside in one or more DNA sequences (Swarup *et al*., 2021).

When genetic diversity is limited, the potential to generate new varieties is also reduced (Syfert *et al*., 2016). Therefore, studying genetic resources in terms of their diversity and genetic variation is important to make decisions focused on their conservation and use. On a historical scale, many crops went through a process of evolution and domestication that shaped the genetic composition of today's crops; nevertheless, only the part of the available genetic resources that covered the needs of humans was selected, which generated a significant loss of genetic variability (Louwaars, 2018).

Conversely, in those unimproved populations, which grew beyond the reach of human selection, there is a wide variation that has not been evaluated or used in genetic improvement programs, this being a large reservoir of genes to increase genetic variation. In the specific case of papaya, the wide geographical distribution of wild populations and the lack of collections in many areas have prevented an accurate assessment of its diversity and genetic structure for conservation purposes (Chávez-Pesqueira and Núñez-Farfán, 2017).

In this sense, the present work aimed to explore the existing information on the genetic resources of papaya (*Carica papaya* L.) in Mexico in terms of its conservation, biological collections, and the potential of outstanding traits to be incorporated into genetic improvement programs.

Origin and studies conducted in Mexico

Papaya is an evergreen plant found in tropical regions; it is a succulent herbaceous plant and has a woody stem that is hollow inside and can measure up to 20 m. The plants can be male, female, and hermaphrodite, with the latter two producing fruit (Paterson *et al*., 2008). The fruits are produced from the upper syncarpous ovary by parietal placentation, which tend to be elongated or pear-shaped depending on the variety (Mora and Bogantes, 2004; Saeed *et al*., 2014).

The first mention of the existence of the papaya (*C. papaya* L.) tree was made in Europe in 1535 by de Oviedo in his book 'Ouiedo de la natural hystoria de las Indias', in which he informed the King of Spain of the discovery of papayas grown between southern Mexico and northern Nicaragua (Lassoudière, 1968). It is believed that it was from this region that the first seeds were taken to Panama, the Dominican Republic, certain Caribbean islands, and parts of South America (Jurandi and Pierre, 2011).

The main hypothesis of papaya origin considers Mesoamerica as the most likely center of its origin, and it is increasingly accepted that *C. papaya* L. had its origin in southern Mexico and Central America because many wild populations are found in this region; therefore, they represent the largest gene pool of genetic variability for evolution, adaptation, and future management of the crop (Fuentes and Santamaría, 2014; Chávez-Pesqueira and Núñez-Farfán, 2017).

In the southern region of Mexico, there are papaya individuals in some family gardens that show phenotypes with intermediate fruits, between wild and cultivated plants (domestication transition through selection or hybridization) (Ruiz-Gil *et al*., 2023). These phenotypes suggest introgression due to occasional mating between different populations (Chávez-Pesqueira *et al*., 2014). Table 1 shows the approaches to the study of the wild and domesticated relatives of papaya in Mexico.

Table 1. Studies conducted in Mexico on the genetic resources of *C. papaya*.

Populations studied	**Collection sites**	**Objective**	**Main results**	**Author**
106 wild populations	From the north to the south of Mexico, following the natural distribution of the species	Diversity and genetic structure of populations and gene flow events	No evidence of the presence of transgenes was found in wild populations and papaya plantations throughout Mexico; there is evidence of gene flow between domesticated and wild papaya	Ruiz-Gil *et al*. (2023).
Not determined	Yucatan Peninsula	Transcriptomic analysis in wild and commercial papayas for tolerance to water deficit stress	The tolerant wild genotype had a greater number of positively regulated genes and a greater number of transcription factors that expressed themselves differentially in response to water deficit stress than the commercial genotype	Estrella-Maldonado *et al*. (2021)
355 individuals from 19 populations	From Tamaulipas to Quintana Roo	Diversity and genetic structure of populations	There is a high genetic diversity and gene flow between populations of *C. papaya* (*r* migration up to 420 km)	Chávez Pesqueira and Núñez Farfán (2016)
222 native individuals	Baja California Sur, Guerrero, Oaxaca, Chiapas, Hidalgo, San Luis Potosí, Tamaulipas, Veracruz, Tabasco, and Campeche	Morphological characterization	Morphological variability shows important differences in the shape, dimensions, and type of the peduncular end in the fruit. Multivariate analyses differentiated between wild and domesticated types collected in family gardens	Hernández-Salinas *et al*. (2019)
81 populations of landrace papaya	11 localities in Baja California Sur	Morphological characterization and conservation	Plants were propagated *in vitro*. Part of this material was transferred to greenhouse conditions for acclimatization and subsequent field planting. Currently, native papaya germplasm is preserved *in vitro* and *ex situ*	Soriano-Melgar *et al*. (2016)
10 populations	Michoacán, Quintana Roo, Tabasco, and Nayarit	Identify, collect, and characterize germplasm of *C. papaya* and *J. mexicana*	Small fruits that corresponded to populations of wild papaya and large fruits were distinguished. Bonetes differ structurally, but their size is close to that of semi-cultivated	Álvarez-Hernández *et al*. (2019)

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Populations studied	Collection sites	Objective	Main results	Author
			papaya populations. Germination ranged from 28.2% to 68.8% and eight of 10 populations germinated at 12 days	
37 outstanding individuals from 12 commercial orchards		Genetic improvement	Identification and characterization of selected plants based on outstanding traits and adapted to the producing area of Michoacán	Álvarez and Tapia-Vargas *et al*. (2019)
109 wild populations, 108 from family gardens, 5 cultivated native varieties, and 449 from external sources	From the north to the south of Mexico, following the natural distribution of the species	Distribution and environmental variables that define the ecogeographic zones of *C. papaya* native to Mexico	*C. papaya* is distributed between 15 and 27° west longitude, at an altitude of 2 to 2 395 m, which shows a wide distribution. In general, it was found in hot and very hot climates with an average annual temperature above 18 °C. No records were found for cold climates. Ten ecogeographic variables define its distribution in Mexico, nine climatic variables and one geophysical variable	Hernández-Salinas *et al*. (2022).
208 wild and 182 cultivated	Guerrero, Oaxaca, Veracruz, Tabasco, and Chiapas	Create a database with georeferencing information on wild and cultivated papaya individuals	The total area of the potential distribution of wild specimens was 114 546.5 km^2; the areas with high potential were located in the Gulf of Mexico (southern Veracruz, Tabasco, and Campeche) and on the coast of Chiapas. The cultivated papaya presented a high potential distribution in three areas: southern Veracruz, coastal Chiapas, and northern Guerrero, making up 185 396.9 km^2	Espinosa *et al*. (2018)
200 individuals of *J. mexicana*	Nayarit, Jalisco, Colima, Michoacán, Guerrero, State of México, Morelos, Veracruz, Campeche, Yucatán, Chiapas, and Oaxaca	Genetic diversity and domestication	There is a high genetic variation in *J. mexicana* and a reduction in genetic diversity derived from human selection on traits related to domestication	Arias *et al*. (2010).

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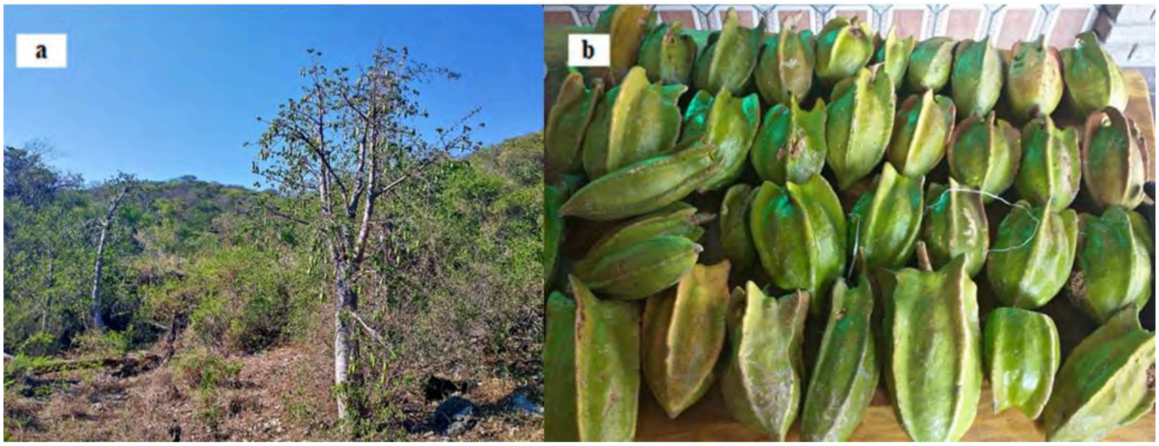
Conservation of wild and domesticated relatives

The Caricaceae family has six genera and 35 species, most of which originated in the Americas (Fuentes and Santamaría, 2014). The only non-American genus is Cylicomorpha, with two species in West Africa; Horovitzia is a genus with a single species (*H. cnidoscoloides*) endemic to the Sierra de Juárez in Oaxaca; in the case of the genus Jarilla, it has three herbaceous species in southern Mexico and Guatemala; for its part, Jacaratia has seven species that are widely distributed in tropical climates; finally, Carica, it only includes the most economically important representative of the family, the common papaya (*C. papaya* L.) (Scheldeman *et al*., 2007; Hernández-Salinas *et al*., 2022).

The somatic chromosomal number in the dicotyledonous genus Carica is 2n=18 (Ibitoye *et al*., 2011). The species inhabit different altitudinal gradients, where there are variations in climate and surrounding or associated vegetation, so they present morphological variations (Figure 1).

Figure 1. a) tree and (b) fruits of *Jacaratia mexicana*. Locality of Amates, Buenavista de Cuéllar, Guerrero, Mexico. Photograph: Martha Isela Croseños Palazin.



Herborized collections are of great importance since they make it possible to determine habitat, diversity, and genetic variation, as well as to make inferences about the origin and distribution of the species (Fuentes and Santamaría, 2014). The National Herbarium of Mexico (MEXU) safeguards 744 herborized specimens of the Caricaceae family collected in South America and Mexico at the Institute of Biology of the National Autonomous University of Mexico (IBUNAM, 2024); these represent the largest collection in the world of this family, of which 694 (93.3%) are from Mexico, where nine species have been identified: Jacaratia, represented with two species and 207 specimens; Vasconcellea, with one species and 35 specimens; Jarilla, with four species and 58 specimens; finally, Horovitzia and Carica, each represented by one species with 31 and 305 specimens, respectively (Table 2).

Table 2. Species of the Caricaceae family reported in Mexico.

Species	State (number of records)	Altitude (m)
Vasconcellea cauliflora	TB (1), OX (8), CH (11), VR (14), PL (1)	90-1 460
Carica papaya	CP (27), CH (58), CM (1), CL (1), GR (9), HG (1), JL (2), EM (1), ML (1), OX (54), PL (17), QR (5), QO (17), TB (19), TP (7), VR (64), YT(16), NDT (5)	10-1 451
Jacaratia dolichaula	CP (1), CH (16), GR (1), OX (5), TB (1), VR (51), NDT (4)	115-380

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Species	State (number of records)	Altitude (m)
Jacaratia mexicana	CP (3), CH (7), CL (2), GR (17), JL (16), EM (2), MH (22), ML (13), NY (3), OX (33), PL (1), VR (5), YT (2), NDT (2)	29-1 409
Jarilla caudata	CL (1), JL (2), MH (1), QR (3)	190-1 800
Jarilla chocola	CH (3), CL (2), JL (8), NY (3), OX (5), SN (1), SR (6)	50-950
Jarilla heterophylla	CM (1), GT (2), HG (1), JL (8), EM (1), MH (5), OX (1), PL (2), QR (2)	700-2 200
Jarilla nana	CM (1), HG (2), JL (3), EM (3), MH (2), PL (2)	2 600
Horovitzia cnidoscoloides	OX (31)	500-1 900

CP= Campeche; CH= Chiapas; CL= Colima; GR= Guerrero; JL= Jalisco; EM= State of Mexico; MH= Michoacán; ML= Morelos; NY= Nayarit; OX= Oaxaca; PL= Puebla; YT= Yucatán; QR= Querétaro; HG= Hidalgo; SN= Sonora; SL= Sinaloa; QO= Quintana Roo; VR= Veracruz; TP= Tamaulipas; GR= Guerrero; GT= Guanajuato; TB= Tabasco; NDT= not determined.

On the other hand, field collections play an initial role since they make it possible not only to conserve germplasm in a natural environment for a long time but also facilitate its characterization, evaluation, and propagation (Ramírez-Galindo *et al*., 2016). In Mexico, 222 specimens of *C. papaya* collected in different regions of the country are preserved in an open field germplasm bank under the direction of the papaya network of the National System of Plant Genetic Resources for Food and Agriculture (SINAREFI, for its acronym in Spanish), of which 109 are from wild populations, 108 were collected in family gardens and five belonged to cultivated native varieties.

They are currently kept in the collection of the College of Postgraduates, Veracruz Campus (Hernández-Salinas *et al*., 2022); this collection has been characterized: the length (cm), diameter (cm), length/diameter ratio, pulp thickness (cm), diameter of the central cavity (cm), and edible volume (cm^3) and qualitative variables that included fruit shape, shape of the peduncular end, shape of the distal end, prominence of edges, shape of the central cavity, and color of the pulp were measured in the fruit; the results indicated that there are significant differences (*p*# 0.01) in all the morphological characteristics studied; the multivariate analyses showed the differences and similarities between wild and domesticated genotypes collected in family gardens (Hernández-Salinas *et al*., 2019).

In other countries, such as the United States of America, Colombia, Ecuador, Cuba and Brazil, efforts have been made in terms of the conservation of wild and domesticated relatives in germplasm banks; to this end, valuable papaya materials have been collected in their own territory and in other countries of Latin America; these banks have significantly boosted papaya genetic improvement programs in the nations that protect them (Dantas *et al*., 2000; d'Eeckenbrugge *et al*., 2003; Alonso *et al*., 2008; Valencia *et al*., 2010; Rodríguez *et al*., 2014; USDA, 2024). Nonetheless, information on the number of accessions and origin of species conserved in such banks is scarce.

Importance and potential for genetic improvement

In commercial terms, papaya has a very important role since, in 2022, Mexico had a production of 1 196 300 t, with a production value of $7 472 256.00 (mxn), and the country was characterized by being the largest supplier of fresh fruit to the United States of America with 198 639 t, which represented 85% of its imports, United States Department of Agriculture (USDA, 2022); Agri-food and Fisheries Information Service (SIAP, 2023). To meet demand and increase productivity, varieties that respond to the particular conditions of each region are needed; thus, wild and domesticated relatives of papaya can be a source of genes to transfer to elite varieties through introgression.

Among the main traits that have been studied as a target for selection under domestication in papaya are lower tree height to facilitate harvesting, fruit size and enlargement of the ovarian wall (pulp), types of sex, morphology, and seed germination (Manshardt, 2014). However, currently,

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the demands increase in the face of global challenges that affect productivity, accessibility, and nutritional quality.

In this context, species of the genus *Vasconcellea* of the family Caricaceae have a wide potential for genetic improvement; d'Eeckenbrugge *et al*. (2014) report that they possess genes for resistance to important diseases, cold resistance, and monoecy, which are absent in the common papaya genome. It has been reported that Andean species, such as *V. cundinamarcensis*, have a very high proteolytic activity compared to *C. papaya*, where it was also observed that some crosses of *V. heilbornii* and *V. stipulata* showed promising levels of papain activity (Kyndt *et al*., 2007).

Genetic resistance to papaya ringspot virus-potyvirus (PRSV-P) has also been identified in *V. cauliflora*, which has been introduced through direct crosses to *C. papaya* (Yanthan *et al*., 2017). Nevertheless, direct crosses can have compatibility barriers, such as the development of embryoless F1 seeds and endosperm-free F1 seeds, which is why Kumar and Tripathi (2016) proposed another transfer bridge, crossing *V. cundinamarcensis* x *V. parviflora*, where F1 individuals are then pollinated with *C. papaya* in order to obtain hybrids resistant to the virus, or crosses between *V. pubescens* x *V. parviflora* and then with *C. papaya* (Drew, 2014).

Conservation challenges

Papaya genetic resources are at risk of loss due to habitat destruction (Chávez-Pesqueira *et al*., 2014) or introgression of improved genes into wild populations (Ruiz-Gil *et al*., 2023). Other factors that seem to be negatively affecting are the pollination system and the short life cycle of *C. papaya*, which impact its genetic diversity, threatening the persistence of its natural populations in the place of origin, as well as its genetic reservoir (Chávez-Pesqueira *et al*., 2014).

Therefore, conserving the natural habitats of wild populations is very important to ensure the necessary levels of genetic diversity and maintain evolutionary potential (Chávez-Pesqueira *et al*., 2014) since species such *V. cundinamarcensis* and *V. microcarpa*, which have endemic populations or populations with restricted distribution, are very vulnerable to genetic erosion or even extinction (Scheldeman *et al*., 2011).

Likewise, it has been reported that the areas of natural occurrence of *Vasconcellea* species are subject to increased pressure from grazing, burning, and the extension of the agricultural frontier, which often leads to a decrease in wild populations of species of this genus (Scheldeman *et al*., 2011). In addition to the above, the lack of representation of genetic variability in germplasm banks puts the distribution and diversity of species at risk; for example, Arias *et al*. (2010) studied the genetic variation of *J. mexicana* populations and determined high levels of genetic diversity in wild populations of southeastern Mexico, which also indicates a wide intraspecific variation; however, it is not represented in national germplasm banks.

Conclusions

There is valuable information on the conservation and potential of outstanding traits of papaya genetic resources in Mexico since different studies have been carried out on the variation, conservation and evolutionary dynamics of these resources. Nonetheless, there is still genetic variation in wild relatives and local populations that has not been studied, quantified, and valued. Therefore, to date, there is not enough information on the potential of these genetic resources for their use in genetic improvement.

These genetic resources are at a high risk of genetic erosion and extinction due to anthropogenic activities and are poorly represented in national germplasm banks, which are of vital importance for the conservation and research of papaya genetic diversity. Therefore, it is necessary to take actions for the conservation of these resources in their natural habitats, which is the most efficient way to conserve populations.

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