Morphological and genetic variability of chili pepper (*Capsicum annuum* L.) populations from northern of Mexico

Variabilidad morfológica y genética de poblaciones de chile (*Capsicum annuum* L.) del norte de México

Variabilidade morfológica e genética de populações de pimenta (*Capsicum annuum* L.) do norte do México

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Abstract

This study investigated the genetic and morphological variability of five domesticated chili varieties (Árbol, Güerito, Mirasol, Negro and Alcalá) and one wild variety (chiltepín) from Chihuahua, Mexico. Morphological evaluation was carried out according to the International Plant Genetic Resources Institute, combining correspondence analyses and Chi-square tests. Genetic variability was determined using the RAPD technique; a dendrogram was constructed, and genetic diversity among populations was estimated using principal coordinate methods, Shannon index, and permutational multivariate analysis. The morphological analysis revealed significant variations, while the genetic analysis, using the RAPD technique, showed 79.5 % polymorphism, indicating considerable diversity among the varieties. The dendrogram revealed the presence of three groups, highlighting chiltepín as potential ancestor of the domesticated varieties. The study emphasizes the importance of conserving and improving these plant genetic resources.

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Resumen

Este estudio investigó la variabilidad morfológica y genética de cinco variedades de chile domesticadas (Árbol, Güerito, Mirasol, Negro y Alcalá) y una silvestre (chiltepín) de Chihuahua, México. La evaluación morfológica se realizó de acuerdo con el Instituto Internacional de Recursos Fitogenéticos, combinando análisis de correspondencias y pruebas de Chi cuadrada. La variabilidad genética se determinó con la técnica RAPD, construyéndose un dendrograma y estimándose la diversidad entre poblaciones mediante coordenadas principales, índice de Shannon y análisis multivariado permutacional. El análisis morfológico mostró variaciones significativas, mientras que el análisis genético, reveló un 79,5 % de polimorfismo, indicando una gran diversidad entre las variedades. El dendrograma reveló la presencia de tres grupos, destacando al chiltepín como un posible ancestro de las variedades domesticadas. El estudio resalta la importancia de conservar y mejorar estos recursos fitogenéticos.

Palabras clave: chiltepín, RAPD, diversidad genética, descriptores morfológicos

Resumo

Este estudo investigou a variabilidade genética e morfológica de cinco variedades de pimenta domesticadas (Árbol, Güerito, Mirasol, Negro e Alcalá) e uma variedade selvagem (chiltepín) de Chihuahua, México. A avaliação morfológica foi realizada de acordo com o Instituto Internacional de Recursos Genéticos Vegetais, combinando análises de correspondência e testes de Qui-quadrado. A variabilidade genética foi determinada pela técnica RAPD; foi construído um dendrograma e a diversidade genética entre populações foi estimada através dos métodos de coordenadas principais, índice de Shannon e análise multivariada permutacional. A análise morfológica revelou variações significativas, enquanto a análise genética, utilizando a técnica RAPD, mostrou 79,5 % de polimorfismo, indicando considerável diversidade entre as variedades. O dendrograma revelou a presença de três grupos, destacando o chiltepín como um possível ancestral das variedades domesticadas. O estudo destaca a importância de conservar e melhorar esses recursos genéticos vegetais.

Palavras chave: chiltepin, RAPD, diversidade genética, descritores morfológicos

Introduction

Chili pepper (*Capsicum annuum* L.) is a crop of great economic and cultural importance, with Mexico recognized as its center of domestication and diversification (Aguilar-Meléndez *et al*., 2018). The extensive genetic diversity of *C. annuum* has resulted in numerous landraces and cultivated varieties adapted to diverse agroecological conditions, particularly in northern Mexico, where environmental factors such as temperature fluctuations, soil composition, and precipitation patterns have influenced their evolution (Aragón-Cuevas & de la Torre, 2015).

The *Capsicum* genus is widely cultivated globally, with *C. annuum* being one of the most extensively grown species (Aguilar-Meléndez *et al*., 2018). In Mexico, chili peppers are a key component of both traditional cuisine and the agricultural economy Aguirre y Muñoz, 2015), ranking second in global production with an annual output exceeding 3.6 million tons and a production value of over 4.5 billion pesos (FAOSTAT, 2019; SADER, 2023). Furthermore, Mexico has the highest genetic diversity of chili peppers, making it a crucial phylogenetic resource for conservation (Contreras-Toledo *et al.*, 2018). However, the introduction of commercial crop varieties and shifts in agricultural practices threaten local cultivars. The expansion of monocultures and habitat alterations are driving genetic erosion, putting these traditionally selected varieties at risk (Hayano-Kanashiro *et al.*, 2016, Rodríguez, 2019).

Understanding the morphological and genetic variability of *C. annuum* populations is essential for multiple reasons. From an agricultural perspective, identifying traits associated with resistance to abiotic and biotic stresses can contribute to breeding programs aimed at improving resilience and productivity (Pérez-Castañeda *et al.*, 2015); Constantino *et al.*, 2020). Additionally, preserving genetic resources is vital to maintaining biodiversity and ensuring the sustainability of chili cultivation in the face of climate change and pest pressures (Votava *et al.*, 2005). Therefore, this study aims to assess the morphological and genetic diversity between domesticated and wild varieties of *C. annuum* populations from northern Mexico by analyzing key traits, and genetic markers.

Materials and methods

Collection of plant material

In 2023, fruits from domesticated and wild chili varieties were collected from municipalities in Chihuahua (Table 1). Three samples of fresh red fruits were gathered from each municipality, transported to the MAFFP laboratory at the Autonomous University of Chihuahua, and left to dry at room temperature (24±2°C). Healthy, uniformly sized seeds were selected and stored at 4°C for future use.

Table 1. Geographical and climatic characteristics of chili pepper varieties.

Samples	Municipalities	GL	MASL	CT	MAP (mm)	MAT (°C)
Chiltepin (CHCH)	Chínipas	27°24′0″N, 108°32′0″W	555	Dry semi-humid	781.7	23.8
Alcala (Alc) & Arbol (A)	Aldama	28°35′40.92″N, 105°34′15.6″W	1,119	Desert	318	19.5
Negro (N)	Julimes	28°32′0″N, 105°3′0″W	1,700	Hyper-arid	60	18.3
Mirasol (M) & Güerito (G)	Delicias	28°11′36″N, 105°28′16″W	1,170	Semi-arid	334	18.8

GL= geographic location, MASL = meters above sea level, CT = climate type, MAP = man annual precipitation, MAT = mean annual temperature.

In vitro germination and seedling production

Viable seeds were disinfected with a 10 % sodium hypochlorite solution for 30 minutes and then rinsed with sterile water. After disinfection, the seeds were incubated in an acidic solution at 24 ± 1 °C for 48 hours, then dried on sterile paper. Twenty-five seeds were placed in each of the ten Petri dishes with sterile filter paper, moistened with sterile water, and sealed. The dishes were placed in a germination chamber with a 16-hour light/8-hour dark photoperiod at 25 ± 1 °C for germination, and the seedlings were ready for transplantation after 20 days. For seedling production, all *in vitro* germinated seeds were placed in germination trays with peat moss and compost substrate, then kept in a chamber at 24 ± 1 °C with a 16-hour light/8-hour dark photoperiod. Watering occurred every 3 days until the plants developed eight true leaves. Domesticated chili seeds undergo the same disinfection process as wild varieties. After sterilization, seeds were sown in trays, each cavity containing

two seeds, and watered until they developed eight true leaves. The seedlings were then transferred to small pots with a soil and peat moss mix, placed in a greenhouse, and watered and fertilized every 3 days for 12 weeks using a nutrient solution (1.5 $g.L^{-1}$ of 12-61-00 (N-P-K), 1.5 $mL.L^{-1}$ of Ca, and 1.5 $g.L^{-1}$ of 18-18-18 (N-P-K). Additionally, 3 $mL.L^{-1}$ of Nutrisorb®, 2 $mL.L^{-1}$ of Radigrow®, and 3 $mL.L^{-1}$ of ATPUP®).

Morphological characterization

Morphological characterization was done using the International Plant Genetic Resources Institute (IPGRI, 1995), focusing on qualitative traits at the seedling, plant, inflorescence, and seed stages. The traits examined included hypocotyl and stem pubescence, cotyledon leaf color and shape, stem and seed color, anthocyanin presence, growth habit, branching and leaf density, leaf color and shape, flower position, fruit shape at bloosom end.

Sample preparation and DNA extraction

Leaf samples were collected from 12-week-old chili plants. For DNA extraction, 200 mg of leaf tissue was macerated and extracted by CTAB (cetyltrimethylammonium bromide) technique as suggested by Michiels *et al*. (2003) with some modifications. Genetic material was purified using the Zymo Research DNA Clean & Concentrator™-5 kit following the manufacturer's instructions. DNA purity and concentration were evaluated using a Nanodrop 2000 spectrophotometer (Thermo Scientific, Massachusetts, USA). DNA concentration was adjusted to 50 $ng.\mu L^{-1}$ for use in the RAPD technique. Only extractions with a 260/280 ratio between 1.8 and 2.0 were used to ensure genomic DNA integrity, verified through 2 % agarose gel electrophoresis.

RAPD analysis

For RAPD analysis, primers OPF 05 (Lanteri *et al*., 2003), MFG 17 (Hermosillo-Cereceres *et al*., 2008), OPA 02 (Bobadilla *et al*., 2017), OPA 07 and OPB 11 (Bhadragoudar & Patil, 2011), OPA 20 (González-Jara *et al*., 2011) and AF 20 (Adetula, 2006) were selected based on their ability to generate a higher number of polymorphic bands. The RAPD amplification was performed according to the methodology proposed by Khan *et al*. (2010), with modifications. A lettuce sample was included as an out-group. Amplified DNA was visualized on a 2 % agarose gel using a photo-documenter (KODAK 1D 3.6). Electrophoresis was carried out at 70 V for 120 min.

Statistical analysis

Statistical correspondence analysis was performed on morphological descriptors using RStudio (version 1.2.5033), and Chi-square tests were conducted to assess statistical differences ($p < 0.05$). For RAPD analysis, a binary matrix was created based on the presence or absence of amplified bands. A dendrogram was constructed using.

Nei genetic distance and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm were used to visualize genetic relationships (Oksanen *et al*., 2020). Principal Coordinate Analysis (PCoA) and the Shannon index were used to analyze genetic diversity. Diversity differences were evaluated using the Kruskal-Wallis test ($p < 0.05$), followed by a PERMANOVA with 999 permutations to assess RAPD profile differences.

Results and discussion

Qualitative morphology

Morphological characterization is considered a crucial step in defining and classifying germplasm (Ratna *et al.*, 2024). Our results confirm that the multiple qualitative descriptors presented statistically significant differences among *C. annuum* varieties evaluated in this study (Figures 1a & 1b). These differences, detected through correspondence analysis and Chi-square tests, reflect the intrinsic genetic variability of the analyzed varieties. Phenotypic diversity, showed highly significant differences, with p-values below 0.001 in descriptors such as cotyledonous leaf shape ($p = 0.00119$), stem color ($p < 0.001$), anthocyanin at the node ($p = 0.00022$), stem pubescence ($p < 0.001$), growth habit ($p < 0.001$), branching density ($p < 0.001$), leaf color ($p = 0.00020$), leaf shape ($p < 0.001$), flower position ($p < 0.001$), fruit shape ($p < 0.001$), fruit shape at the blossom end ($p < 0.001$), and seed color ($p < 0.001$). These results demonstrate the heterogeneity among the domesticated chili varieties and the wild chiltepin variety, as each analyzed descriptor is key to understanding how these chili species have adapted to different environmental and cultivation conditions. Previous studies have highlighted that morphological traits such as pubescence are important adaptations to specific cultivation conditions, although their variability might be limited in certain genetic groups. This trait is associated with resistance to pests and diseases and reduced water loss, which is particularly relevant in dry climates (Bobadilla-Larios *et al*., 2017).

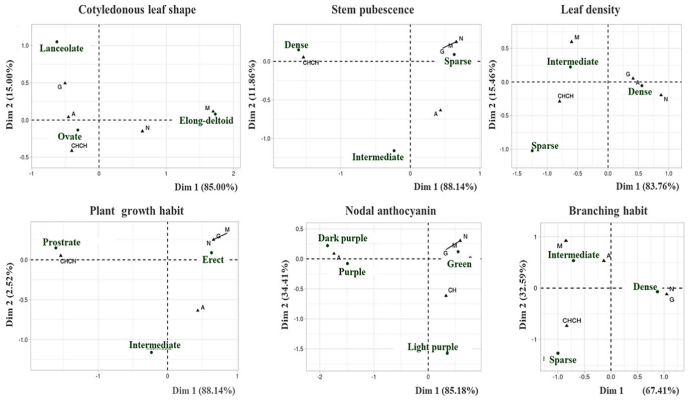

Figure 1a. Morphological treats (cotyledonous leaf shape, stem pubescence, leaf density, branching and plant growth habit, nodal anthocyanin, and branching habit) of domesticated and wild chili varieties.

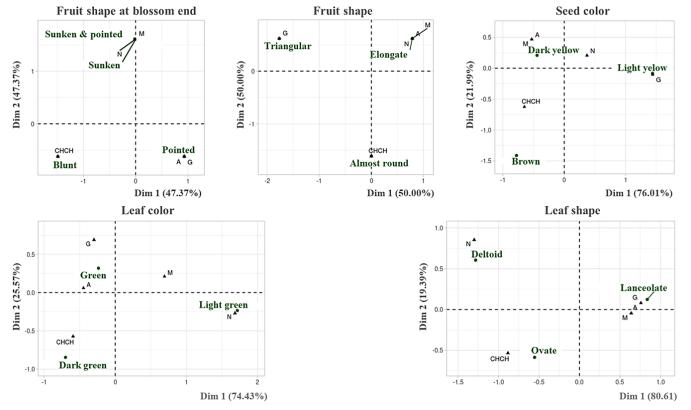

Figure 1b. Morphological treats (fruit shape at blossom end, fruit and leaf shape, seed and leaf color) of domesticated and wild chili varieties.

Variations in leaf shape are linked to adaptive strategies and productivity under diverse environmental conditions (Carrillo-Montoya y Vargas-Rojas, 2023). These results reinforce leaf

morphology as a key indicator in taxonomy and crop genetic improvement.

Stem color has been associated with anthocyanins, which possess antioxidant properties and are influenced by genetic and environmental factors focused on abiotic stress resistance (Bobadilla-Larios *et al*., 2017). Additionally, highly differences in branching density reflect ecological adaptations as well as leaf density, although marginal differences was detected in the last trait (p = 0.02498). These traits are important for optimizing agronomic management, such as planting density, phytosanitary management, photosynthesis potential, and fruit production to maximize yield in various cultivation systems (Bobadilla-Larios *et al*., 2017; Carrillo-Montoya y Vargas-Rojas, 2023). These adaptations may be associated with specific light and temperature conditions. Leaf color has implications for selecting varieties suited to different climatic zones, as do other described traits.

Fruit shape diversity reflects both natural and artificial selective pressures. In the commercial context, preference for specific fruit shapes can significantly influence product acceptance in local and global markets, making this trait indispensable for differentiating chili species (Figure 2) (Bobadilla-Larios *et al*., 2017; Carrillo-Montoya y Vargas-Rojas, 2023).

Figure 2. Morphology of chili fruits varieties. Domesticated varieties: a = Alcalá, b = Árbol, c = Negro, d = Güerito, e = Mirasol, and wild variety: f = Chiltepin.

Characterization of RAPD markers

The molecular characterization of six chili varieties generated 181 amplified bands, of which 144 were polymorphic (79.5 %). Additionally, the number of amplified fragments ranged from 21 (OPB11) to 37 (MFG17), and the polymorphism range varied from 64 % for OPF05 to 96 % for AF20 (Table 3). In contrast, a study using 10 primers obtained only 45 polymorphic bands, ranging from 3 to 7 bands per primer (Votava *et al*., 2005). Achieving a high percentage of polymorphisms could reveal greater significant genetic variability within the studied population (Figure 3).

Table 3. Random primers used, number of PCR amplified bands and polimorphism.

Primers	Number of Amplified Bands	Polymorphic Bands	Polymorphism (%)
MFG17	37	33	89
OPA07	24	20	83
OPF05	25	16	64
OPA20	24	18	75
OPA02	23	16	70
OPB11	21	15	71
AF20	27	26	96

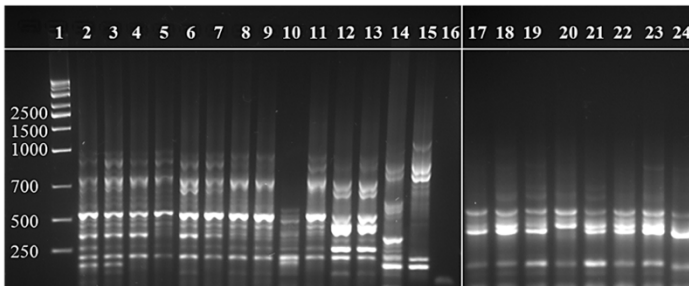

Figure 3. PCR-RAPD amplification of six chili pepper varieties using primers OPB11 (a) and OPF05 (b). (a) Lanes: 1) MPM, 2-13) duplicate samples of domesticated chili (A, G, M, N, Alc) and wild chili (CHCH), 14-15) duplicate lettuce samples (L, outgroup), 16) negative control. (b) Lanes: 17-28) duplicate samples of domesticated chili (A, G, M, N, Alc) and wild chili (CHCH), 29-30) duplicate lettuce samples (L, outgroup), 31) negative control, 32) MPM.

Bobadilla-Larios *et al*. (2017) reported 45.45 % polymorphism for the OPA02 marker, whereas González-Jara *et al*. (2011) reported 40 % for the same marker and 81.25 % for OPA20. In contrast, the results obtained in this study showed 70 % polymorphism for OPA02 and 75 % for OPA20 (Table 3). In a similar study on *C. annuum* L. genotypes, Bhadragoudar & Patil (2011) reported 88 % polymorphism for the OPA07 molecular marker, comparable to our results (83 % polymorphism). Meanwhile, polymorphism with the OPB11 marker was reported to be 66.6 %, compared to polymorphism with 71 % in our study. The distance matrix offers a clear view of the genetic diversity, with values ranging from 0.2588 to 0.9429. The closest genetic distance was between Güerito and Arbol samples, while the most distant relationship was between Arbol and lettuce samples., where Lettuce was used as an out-group sample.

In 2017, Bobadilla-Larios *et al.* reported low genetic variability (0.74 and 0.96) in their study, with the most significant variability among the Ancho, Calera, and Mirasol Don Luis SLP chili varieties. Another study reported a range of genetic variability from 0.20 to 0.94 (Bhadragoudar & Patil, 2011). A study of chili samples in Nigeria found a genetic distance (Jaccard coefficient) ranging from 0.21 to 0.88, with an average of 0.61 (Adeyemo & Lawal, 2020). These findings align with our results.

A dendrogram was constructed, resulting in three groups (Figure 4a). This dendrogram was generated based on the genetic relationships among the analyzed varieties, including domesticated chili cultivars and the wild Chiltepin chili variety. Group A includes the lettuce population, with an average genetic similarity value of 0.70 compared to the Chili pepper varieties. Since this species does not belong to the *Capsicum* genus, it was considered an out-group sample, indicating that this result is consistent. Meanwhile, Group B consists solely of the Chiltepin chili variety, with an average genetic distance of 0.61. This result confirms that Chiltepin is the potencial ancestor of other chili varieties, as mentioned by Votava *et al*. (2005), González-Jara *et al*. (2011) and Hayano-Kanashiro *et al*. (2016). The remaining domesticated chili populations were grouped into Group C, forming two subgroups. Alcala and Negro chilies represented the first subgroup (C.1). In contrast, the second subgroup (C.2) was represented by the Arbol, Güerito, and Mirasol chili samples, similar to groups F and G reported in another study (Votava *et al*., 2005). Other studies have grouped between 14 and 18 groups (Votava *et al*., 2005; Bhadragoudar & Patil, 2011). Meanwhile, other authors

have reported between 2 and 4 groups (Bobadilla-Larios *et al*., 2017; Mbasani-Mansi *et al*., 2019; Constantino *et al*., 2020).

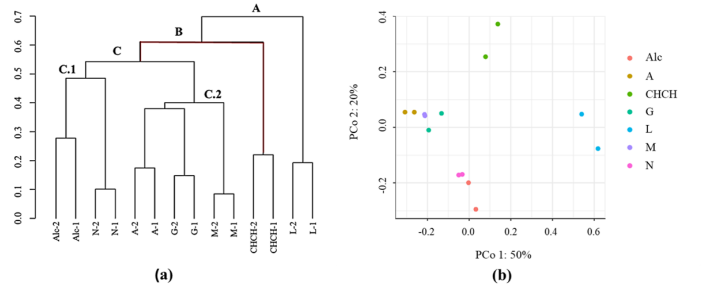

Figure 4. Dendrogram (a) and Principal Coordinates Analysis [PCoA] (b). Where: Alc = Alcala, N = Negro, A = Arbol, G = Güerito, M = Mirasol, CHCH = Chiltepin, L = Lettuce (out-group).

A principal Coordinates Analysis (PCoA) was conducted using distances calculated by Nei's algorithm (Figure 4b). In this analysis, the first three principal components explained 89 % of the variation in the dispersion of *Capsicum annuum* L. varieties. Specifically, Principal Component 1 (PCo1) accounted for 50 %, Component 2 (PCo2) explained 20 %, and Component 3 (PCo3) explained 19 % of the variance.

In Figure 4b, clear discrimination can be observed among the *Capsicum annuum* L. chili species, including Alcala, Negro, Güerito, Mirasol, Arbol, and the wild Chiltepin chili. The results of this experiment are consistent with those reported for Coordinate 1, with 45 % (Pacheco-Olvera *et al*., 2012). These findings strongly support the topology observed in the dendrogram Figure 4a.

The Permutational Multivariate Analysis (PERMANOVA) was performed using a reduced model to evaluate differences among the samples based on the distance matrix. The analysis examined whether significant differences existed in the multivariate structure among the varieties, considering variability within groups and their similarity or dissimilarity. The analysis revealed that the sample factor had 6 degrees of freedom, a sum of squares value of 1.98, and a coefficient of determination of 0.9445, explaining 94.45 % of the total variation. The p-value (0.001) indicates significant differences among all the samples analyzed. Identifying and correctly interpreting the genetic relationships among the different genotypes studied is crucial to these experiments.

Our study reveals that the genetic variation of chili pepper varieties under investigation is directly related to their shared geographical characteristics, particularly the domesticated varieties that exhibit closer genetic proximity. This genetic proximity is supported by the formation of group C and subgroups C.1 and C.2 in the dendrogram (Figure 4a).

Genetic diversity of chili varieties

The Shannon index was used to calculate genetic diversity, obtaining values higher than 4.3 for this index. A high index value indicates greater diversity among the analyzed samples (Figure 5), implying more alleles or genetic variability. The lowest value was 4.31 for the lettuce sample, while the highest value was attributed to the Arbol chili, with a value of 4.58. The p-value was 0.05227 (slightly above the commonly used significance level of $p < 0.05$). This clear separation of populations can also be observed across different axes in the Principal Component Analysis, accounting for 89 % of the variability. Therefore, this variety's remarkable genetic variability is attributed to its geographical location in the municipality of Chínipas, Chihuahua, Mexico, at an altitude of 555 meters above sea level. It has a warm-temperate climate and an average annual precipitation of 781.7 mm, which significantly differs from the domesticated populations.

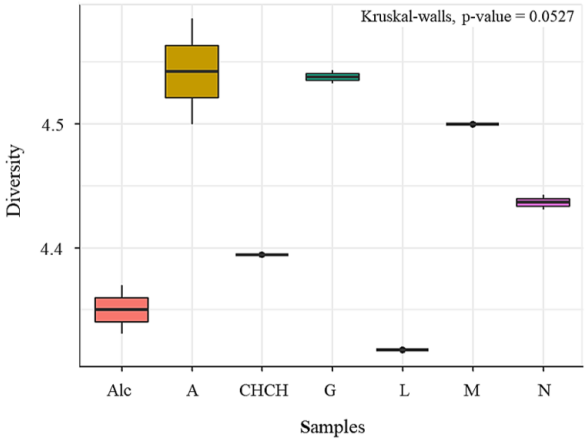

Figure 5. Diversity of analyzed chili varieties according to the Shannon Index. Where: Alc = Alcala, A = Arbol, CHCH = Chiltepin, G = Güerito, L = Lettuce, M = Mirasol, N = Negro.

Conclusions

This study highlights the genetic variability between domesticated and wild chili varieties, offering valuable insights for conservation and breeding. Chiltepin, the potential ancestor of cultivated chilis, shows significant genetic diversity, supporting genetic improvement efforts for higher yields. Morphological differences demonstrate adaptability and potential for yield, assisting breeding under different conditions. The research emphasizes the importance of using multidisciplinary approaches, including morphological, agronomic, and molecular analyses, to understand species dynamics, population evolution, and ecological interactions.

Acknowledgments

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