Exploring genetic diversity of lowland avocado as a genetic reservoir for breeding.

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Short Report

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Abstract

The avocado (*Persea americana* Mill.) is highly valued worldwide for its desirable nutritional properties and broader applications in the oil and pharmaceutical industry. Despite northwestern Mexico, with a tropical semi desert climate, is not considered as part of the avocado origin center in Mexico, it possesses a high morphological diversity of avocado fruits. In an effort to provide more information about the diversity present in this region and at the same time, to support a more efficient production of avocado in this climate, this study characterized the genetic diversity of avocado trees growing at northwestern Mexico. Genetic diversity was estimated by using eight microsatellite loci. 45 seed-derived trees, with contrasting fruit morphology were identified. Results showed a high level of genetic diversity with 11.5 alleles per locus, a polymorphic index content of 0.75, and observed and expected heterozygosity values of 0.58 and 0.79, respectively, these values were similar to those observed in germplasm banks and genotypes from centers of origin. Clustering analysis assigned local genotypes to six clusters but did not provide a clear separation among avocado races, suggesting that local genotypes are a result of racial hybridization. Interestingly, avocados from the Mexican race and the commercial variety Hass clustered into two different groups. Despite not being considered a center of origin, results confirm an extensive diversity in northwestern Mexico, encouraging further exploration and preservation of genotypes with desirable traits to future breeding programs for the selection of local genotypes adapted to a lowland tropical climate.

1. Introduction

The avocado (*P. americana* Mill.) is an economically important tropical fruit in the international market. In North and South America, its production is concentrated in 12 countries. Mexico is the main producer with 35%, followed by Chile and the United States with 9 and 8%, respectively. Due to its importance as a staple food, this species has been subjected to a long domestication history. During this process, the species evolved not only by natural hybridization, but also by artificial selection and controlled crosses, which have resulted in individuals with diverse phenotypes that combine elements from three races distinguished according to their origin and morphology (*drymifolia*, Mexican; *guatemalensis*, Guatemalan; and *americana*, West Indian) (Ayala-Silva and Ledesma 2014; Guzmán et al. 2107; Boza et al. 2018).

In Mexico, avocado is grown in many different intensive agricultural systems, ranging from commercial orchards to backyard gardens, that serve as important centers of experimentation, plant introduction, empirical improvement and sanctuaries of unique genetic diversity that harbor novel genes of potential use in breeding programs. Given that the avocado is an open-pollinated species, it contains considerable genetic variability with almost unlimited possibilities for utilization (Guzmán et al. 2017); a wide diversity of germplasm increases the number of alleles available to be used in the generation of new cultivars (Ayala-Silva and Ledesma 2014). Considering its high diversity, the avocado germplasm of Mexico has provided the basis of breeding programs in other countries, emphasizing the importance of exploration, classification and preservation of native to implement breeding programs.

Hass is the commercially preferred variety of avocado, and it is successfully cultivated in uplands with a temperate climate. In Mexico, 90% of Hass production is centered in Michoacán, Jalisco, and the state of Mexico, which provide optimal climatic conditions for this variety. However, in the rest of the country there are many other varieties that are locally adapted to lowland and more tropical conditions (Guzmán et al. 2017). In a previous study, our research group found high genetic variation and tocopherol content in a small group of seed-derived avocado trees growing on backyards with no agronomic management (Peraza-Magallanes et al. 2017). These local varieties are morphologically diverse and represent a promising source not only for plant breeding, but also as cheaper substitutes for biotechnological products in the cosmetic and pharmaceutical industries (Espinosa-Alonso et al. 2017). Despite efforts in avocado conservation, germplasm banks are mostly focused on commercial varieties and core collections near to the center of origin of avocado located at southeast Mexico and Guatemala (Guzmán et al. 2017). People have cultivated and used avocado as a food since Spanish pre-conquest; evidence suggests that avocado has been subject to selection by fruit size as early as 7000 B.C. (Smith 1966). Since then, human-mediated avocado dispersion has strongly influenced the presence of avocado trees outside their natural range limits. In recognition of the potential of local varieties in northwestern Mexico, analyzing the genotypes present in the region is crucial in order to identify appropriate genotypes that might succeed locally and to preserve them in germplasm collections. Despite northwestern Mexico is not considered as center of origin, this study reports high genetic variation in local avocado genotypes from northwestern Mexico, with a potential mixture between West Indian and Mexican races. This information will benefit future breeding programs for the selection of adapted genotypes, but also to preserve the genetic diversity of local germplasm adapted to lowland and tropical climate.

2. Material And Methods

2.1 Plant Material

Forty-five non-commercial and seed-propagated avocado trees derived from local plantations with unknown racial origin, six Mexican landrace individuals, and one clonally propagated commercial cultivar (Hass) were selected for this study. Local avocados were considered as our target population and Mexican-race and Hass trees served as controls. The collection was chosen primarily for its differences in tree and fruit morphology. The sampling locations of collections are described in Table 1.

It is important to note that local avocados are grown without agronomic management. Racial origins are mostly unknown, and even people who own these trees do not know where they came from. Figure 1 shows morphological fruit variation of 26 local accessions and the cv. Hass. The remaining individuals were not included due to the lack of fruit during the years of collection (2014-2015).

2.2 Genetic characterization

Total genomic DNA was isolated from young leaves using 3% cetyltrimethylammonium bromide (CTAB) according to Doyle and Doyle (1987) with small modifications. Briefly, tissue was macerated with a plastic pestle in a microcentrifuge tube containing 800 µL of CTAB buffer and incubated to 65 ºC for 2 h.

The homogenate was extracted with approximately 0.6 volumes of chloroform/isoamyl alcohol (24:1 v/v) and centrifuged at 13,000 rpm for 10 min to separate phases. DNA was then precipitated at -20 ºC during 2 h with 0.7 volumes of isopropanol and then centrifuged at 13,000 rpm for 10 min. The DNA was resuspended in 100 µL of Nano pure water. DNA quality was evaluated on agarose gels and DNA concentrations were determined with a NanoDrop ND-2000 spectrophotometer (Thermo Fisher Scientific, Inc).

Individuals were genotyped at eight highly polymorphic microsatellite loci (AVD.001, AVD.006, AVD.013, AVD.022, AVO.102, LMAV.27, ESTAVT.04 and LMAV.33) as previously described (Ashworth et al. 2004; Gross-German and Viruel 2012). The forward primers were fluorescently labeled with FAM, VIC, and NED (Thermo Scientific). PCR amplifications were performed in 10 µL containing 1X PCR Buffer, 2.0 mM $MgSO_4$, 140 µM of each dNTP, 0.17 µM of each primer, 1 Unit of Taq DNA polymerase (Platinum, Invitrogen) and 10 ng of genomic DNA. Microsatellite loci were amplified on a C1000 Touch BIORAD thermal cycler. The amplification program consisted of 1 min at 94 ºC, followed by 35 cycles of 30 s at 94 ºC, 30 s at 52 ºC and 1 min at 68 ºC, and a final cycle of extension at 68 ºC for 5 min. All microsatellite loci were amplified with the same temperature profile except AVO.102, which was annealed at 53 ºC. PCR fragments were separated by capillary electrophoresis on a 3500 Genetic Analyzer (Thermo Scientific). Microsatellite alleles were visualized and scored in the GeneMarker software (SoftGenetics). Then, the total number of alleles, polymorphic information content (PIC), observed heterozygosity (Ho), and expected heterozygosity (He) were calculated using FSTAT software V 2.9.3.2 (Goudet 2001). In order to investigate the genetic structure of the avocado collections and to organize them into groups based on microsatellite data, a Bayesian clustering analysis implemented in the software STRUCTURE 2.3.4 was used (Pritchard et al. 2000). Two different analyses were performed in STRUCTURE. In the first analysis, controls and local avocados were defined as independent populations. Since controls and local avocados are geographical and sexually isolated, in this analysis, runs were based on the no-admixture model with uncorrelated allele frequencies. In the second analysis, controls were removed and only local avocados were analyzed. Since pollination is potentially possible among local avocados, in this analysis, runs were based on an admixture model with correlated allele frequencies. STRUCTURE runs were carried out with a length of burn-in and MCMC (Markov chain Monte Carlo) of 500,000 each and 500,000 repetitions. Ten independent runs were conducted allowing K (number of populations) to vary from 1 to 12. In order to assess the best K-value supported by the data, the ΔK method described by Evanno et al. (2005) was used through Structure Harvester v. 6.93 (Earl and von Holdt 2012). Genotypes were assigned to the group for which they had the highest assignment coefficient (Q value).

3. Results

The eight microsatellite loci showed high levels of genetic diversity. In total, 108 alleles were detected among the 52 avocado accessions. The mean number of alleles was 13.25 alleles per locus, ranging from 7 in LMAV.27 to 24 in AVD.006 (Table 2). The PIC values ranged from 0.4 in LMAV.27 to 0.9 in AVD.001. These values show that the microsatellite loci used here are highly informative. The Ho ranged

from 0.31 in LMAV.27 to 0.82 in AVO.102. Analyzing the local avocados, a total of 82 alleles were detected, of which 50 alleles were unique to local accessions and 32 were shared with the controls belonging to the Mexican race and cv. Hass. Despite sharing 32 alleles, these results did not support a clear separation between local avocados and controls. The number of private alleles in controls ranged from 0 in AVD.022 to 8 in AVD.006, finding 26 exclusive alleles in the complete set of microsatellite loci. On the other hand, the number of private alleles in local avocados ranged from 1 in LMAV27 to 13 in AVD.006, finding 50 exclusive alleles in the complete set of microsatellites, which doubled the number of exclusive alleles detected in avocado controls (Table 3).

The first analysis in STRUCTURE showed that the local accessions were different from the controls (Fig 2A), except for AVO05, AVO24, AVO25 and AVO74, suggesting that these four accessions could have a Mexican-race origin. The second analysis supported a high genetic structure among local accessions, which were grouped into six clusters (Fig 2B). Pairwise genetic comparisons showed a significant difference among the six groups. The group containing the samples AVO05, AVO24, AVO25 and AVO74 in purple color showed the highest differentiation with respect to the others (Fig 2B).

4. Discussion

Mexico, as a center of origin and avocado domestication, is home to an extensive variety of avocado trees that are adapted to a wide range of climatic conditions (Guzman et al. 2017). These individuals are highly diverse not only in fruit morphology but also in tree structure, pest resistance, and adaptability to environmental conditions. This extensive diversity might provide valuable sources for avocado improvement and biotechnological applications (Peraza-Magallanes et al. 2017; Espinosa-Alonso et al. 2017). The results presented here showed that individuals from northwestern Mexico not only differ from Mexican race but also possess a high variation among them. These findings demonstrate that even in tropical climates, a high diversity exists in avocado species. In Mexico, three avocado races have been distinguished according to their origin and morphology (Mexican, Guatemalan and West Indian). According to fruit morphology and climate preferences, the avocados analyzed here seems to have more similarities with the West Indian race. However, the geographical origin of this race is along the lowlands of southeast Mexico and Central America, which is geographically distant from our sampling sites in northwestern Mexico. Since northwestern Mexico is not considered a center of origin and domestication of avocado, we hypothesize that humans dispersed avocados of the three races to this region. However, only the West Indian race and its hybrids with the other races succeeded at northwestern Mexico, possibly due to similar climatic conditions in the region where West Indian avocados grow naturally. Since human dispersal is difficult to control, avocados from unknown climatic and racial origins may have been imported into this area. Furthermore, since avocado is an open-pollinated species and trees in non-commercial orchards are randomly established alongside other trees with different morphologic characteristics, once the avocado trees are reproductively active, they are frequently cross-pollinated, with a low rate of selfing (Sánchez-González et al. 2020), thereby, increasing their genetic diversity through inter-racial crosses. Identifying localized centers hot spots of diversity of avocado resources is fundamental for the conservation and preservation of genetic reservoirs adapted not only to lowland and

tropical climate but also that exhibit resistance to diseases prevalent in commercial cultivars. Efforts in conservation of avocado genetic resources have been previously reported in south America but these projects have been focused on Mexican and Guatemalan races, leaving aside the west Indian race, which is a promissory avocado resource for lowland and tropical climate conditions (Aleman et al. 2005). It is important to mention that avocados analyzed here were collected in non-commercial orchards, and that the sampling design was arranged to capture most of the diversity present in the study area, which might partially explain the extensive diversity reported here.

Our results confirm previous reports that suggested that avocado species harbor very high genetic diversity (Peraza-Magallanes et al. 2017; Guzman et al. 2017; Juma et al. 2020) and perhaps that northwestern Mexico may be considered as a center of diversity of avocado resources adapted to lowland and tropical climate. Interestingly, a high genetic diversity was found in a very small area, which might suggest complex patterns of reproduction and dispersal of this fruit, as suggested by Galindo-Tovar et al. (2008). Recently, our research group reported high levels of genetic variation and α-tocopherol content in five collections from northwestern Mexico (Peraza-Magallanes et al. 2017). Our genetic diversity results are consistent with the levels of genetic diversity reported for avocados from different geographical regions. For instance, Alcaraz and Hormaza (2007) analyzed 75 accessions from Spain, Mexico, USA, Guatemala, Israel and Honduras. They found a lower number of alleles (9.75) but comparable values of heterozygosity (He=0.76). Gross-German and Viruel (2012) found high genetic diversity in cultivars of avocados from Israel, USA, Spain, Cuba, Mexico, South Africa, Ecuador, Chile, and Australia. Even in small populations recently introduced, high levels of genetic diversity have been reported on trees originated from seeds in Tanzania (Juma et al. 2020). This high genetic diversity in avocado might be due to the high outcrossing rate reported in *P. americana* (Sánchez-González et al. 2020).

In the era of massive DNA sequencing, this work demonstrates that the use of microsatellite markers is a valuable and practical tool to estimate genetic diversity in local avocado with small population size (Juma et al. 2020). The level of polymorphism found was sufficient to detect a very high genetic variation and provides good estimates of relatedness in a very small area with local genotypes. However, given the findings in this work it is justified employing a genomic approach for getting more detail of avocado genetic contents and diversity in this area.

As evidenced before (Guzmán et al. 2017), the molecular analyses of the avocado varieties did not achieve a clear differentiation among the botanical races, which could indicate that the local gene pool in northwestern Mexico is now an interracial mixture. However, it was possible to observe in the first STRUCTURE analysis (Fig 2A) that most of the local accessions were different from the controls, which are of Mexican race origin, collected from a germplasm bank. Interestingly, genotypes AVO05, AVO24, AVO25 and AVO74 clustered into the same group with the controls, suggesting that these four accessions are of Mexican-race origin. The second STRUCTURE analysis with only local accessions supported this hypothesis because the group containing the samples AVO05, AVO24, AVO25 and AVO74 (purple group) showed the highest differentiation with respect to the other local avocado genotypes (Fig. 2B). Genotypes

AVO24 and AVO25 are locally known as “San Miguel” variety, which is considered a local commercial variety that has fruit shape, pulp texture and oil content similar to the Hass variety.

On the other hand, the population structure of local avocados was different from the controls. These findings suggest that local avocados share alleles among themselves and have been accumulating similar allele frequencies due to complex patterns of sexual reproduction, as well as random human dispersal of avocado seeds and seedlings according to local fruit preferences, but also in response to climatic preferences and adaptability of the trees.

Given that local avocados are seed-propagated, the high variation in non-commercial accessions might result from cross pollination during sexual reproduction (Ayala-Silva and Ledesma 2014). High rates of recombination and outcrossing would serve to increase phenotypic and genotypic variation (Sánchez-González et al. 2020). In the clonally propagated variety Hass, morphological variation due to sexual reproduction is prevented.

Given that the avocado germplasm of Mexico has been the basis of breeding programs in other countries, understanding and preserving genetic diversity of *P. americana,* as well as exploring strategies for its conservation are imperative to implement successful breeding programs not only locally but also internationally (Guzmán et al. 2017; Boza et al. 2018).

Since farmers in northwestern Mexico usually grow avocados for their own consumption, avocado production does not represent a significant income for them; however, their nutritional characteristics (Peraza-Magallanes et al. 2017) are attractive to consumers and should encourage commercialization of these avocado varieties either as fresh or industrialized products.

This study reports an extensive and unexplored diversity of avocado genotypes present in northwestern Mexico, encouraging further exploration and preservation of genotypes with desirable traits beyond the identified centers of origin. This information is pertinent to future breeding programs not only for the selection of local genotypes adapted to a lowland tropical climate but also as an alternative for new avocado varieties production.

Declarations

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Conflict of interest:

The authors declare that they have no conflict of interest.

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Tables

Table 1. Geographic location of avocado sampling collections.

Avocado sampling collection	Georeferencing			Classification	Number of accessions
	Latitude	Longitude	Elevation (m)		
NW_PLA	25°36’31”N	108°31’40”O	21	NCO	22
NW_GPM	25°35’09.60”N	108°30’38.4”O	18	NCO	3
NW_VIR	25°36’96.36”N	108°31’29.19”O	18	NCO	3
NW_CTR	25°33’46.73”N	108°27’550.57”O	17	NCO	6
NW_CSB	25°25’29”N	108°25’19”O	14	NCO	4
NW_CHI	25°36’28.65”N	108°31’13.93”O	18	NCO	2
NW_GTO	25°34’00.63”N	108°26’36.18”O	21	NCO	2
NW_PAL	25°24’13.14”N	108°25’13.84”O	8	NCO	1
NW_A	25°28’55”N	108°23’3”O	10	CO	2
MEX	18°55’26.50”N	99°46’04.07”O	2226	GB	6
HASS	19°25’22.80”N	102°05’20.33”O	1794	CO	1

NW; northwestern Mexico, MEX; Mexican race avocados, HASS; commercial variety. NCO: Non-Commercial Orchard, CO: Commercial Orchard, GB: Germplasm Bank

Table 2. Genetic diversity of the avocado genotypes assessed. Exclusive and shared alleles among controls and local avocados are presented.

Locus	A	PA		Shared Alleles	HO	HE	PIC
		Local	Controls				
AVD.006	24	13	8	3	0.81	0.91	0.89
AVD.001	18	9	5	4	0.48	0.91	0.90
AVO.102	17	7	4	6	0.82	0.91	0.88
ESTAVT.04	14	7	3	4	0.66	0.88	0.86
AVD.013	12	6	1	5	0.54	0.77	0.74
LMAV.33	9	3	2	4	0.43	0.81	0.77
AVD.022	8	4	0	4	0.63	0.75	0.71
LMAV.27	6	1	3	2	0.31	0.45	0.41
MEAN	13.5	6.25	3.25	4	0.58	0.8	0.77
TOTAL	108	50	26	32			

A: number of alleles, PA: Private alleles, HO–HE: observed and expected heterozygosity, PIC: polymorphic index content.

Table 3. Genetic diversity of avocado genotypes. Local are avocados collected at northwestern Mexico and controls are avocados from Mexican race and Hass variety. Exclusive and shared alleles among controls and local avocados are presented.

Avocado	n	A	PA	HO	HE	PIC
Local	45	82	50	0.58	0.76	0.73
Control	7	51	26	0.61	0.83	0.72

n: sample size, A: number of alleles, PA: Private alleles, HO–HE: observed and expected heterozygosity, PIC: polymorphic index content.

Figures

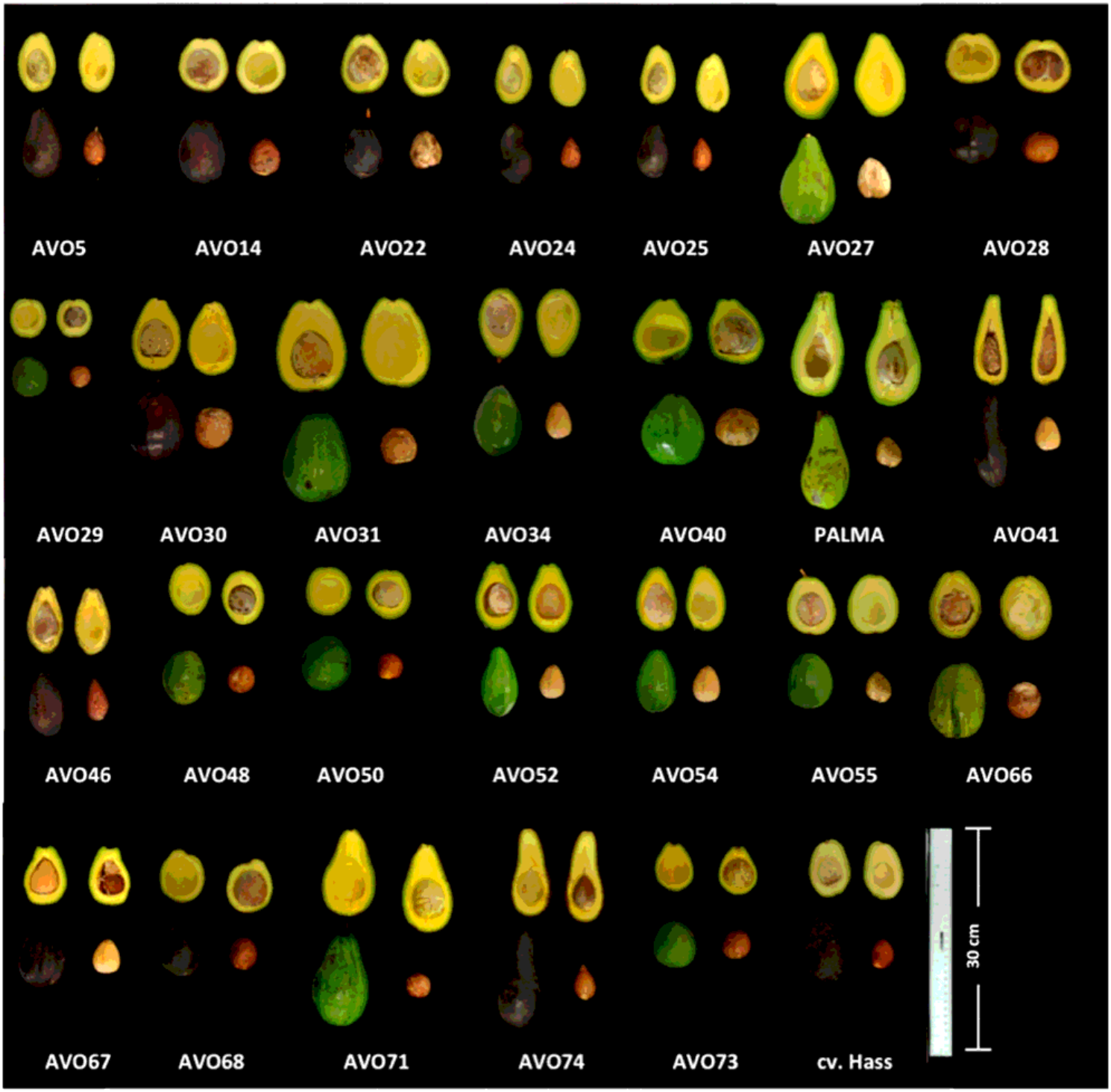

Figure 1

Fruit shape variation of avocado Hass and 26 avocado collections from northwestern Mexico.

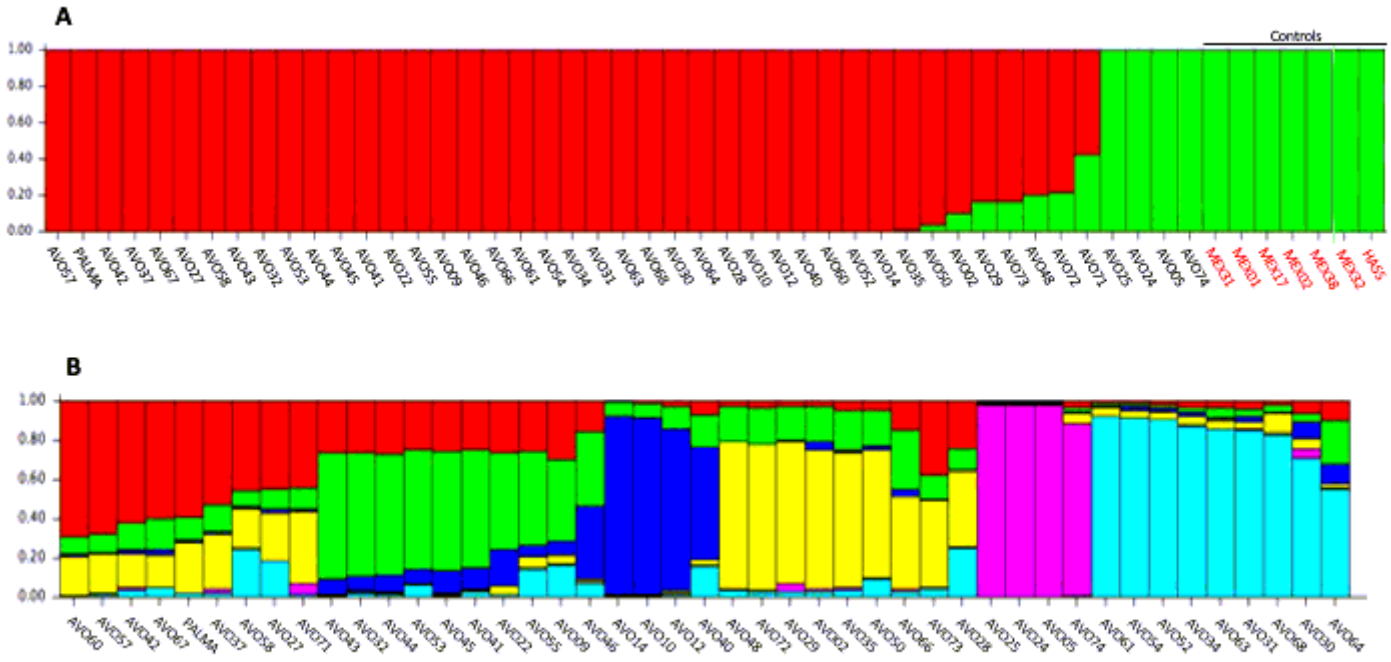

Figure 2

Population genetic structure of A) using no-admixture model and uncorrelated allele frequencies, controls and local avocados from northwestern Mexico were considered in the analysis and B) using admixture model and correlated allele frequencies, only local avocados were considered in the analysis. Vertical bars show individuals, colors are indicative of two groups in A (K=2) and six groups in B (K=6) Y-axis indicates the Q-value or percentage of assignment to each group.