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Genetic Analysis of Peaches Grown by Native Americans in the North American Southwest

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Abstract

Peach (*Prunus persica*) originated in China and was introduced to Central America in the first half of the 16th century by Spaniards. In North America peaches were cultivated by the southwest Native American Tribes including the Navajo, Hopi, and Pueblo as an important food source since at least the early 1600s. Few isolated peach orchards remain in remote canyons and mesa shelves, and are still tended using traditional methods. The purpose of this study was to locate and characterize these plantings in order to understand the genetics of these isolated peach populations. Three distinct regions with peaches were identified, representing lands from Navajo and Hopi Tribes. Seeds were collected from these isolated populations for genetic analysis, and soil type, microclimate and water availability were documented for these sites. Genetic analysis indicates populations from each of the three regions are genetically distinct from modern cultivars, as well as among the three locations. However, several individuals sampled showed outcrossing with modern cultivars. These isolated populations need further characterization for useful traits and should be protected for their unique genetic and cultural significance.

Peach (*Prunus persica*) originated in China 3000BC (Huang et al., 2008) and was spread to Europe via westward movements. Peach cultivation in the Americas began in the16th century by Spanish conquistadors in Central America from where it was spread to Northern America (Bassi and Monet, 2008). Southwest Native American tribes have successfully grown peaches since its introduction to the Americas, making them an important food source along with corn, beans, and squash. The Navajo white peach is noted for its flesh color and small size (Jett, 1977). The peaches were seed propagated over multiple generations, likely forming landraces or seedling varieties where plantings were isolated (Marrow, 1996). Historic orchards appear to have been kept isolated from modern cultivars up until the late twentieth century. However, recent efforts have been taken to replant deceased orchards with modern cultivars in annual Earth Day celebrations (Window Rock Navajo Times, 2007). Consequently, seeds from traditional peach varieties have become scarce.

Peach orchards existed across the Navajo, Hopi and Pueblo Reservations including in what is now Canyon de Chelly National Monument; canyons near Navajo Mountain, Utah; along the San Juan River in New Mexico; around mesa bases in Hopi, Arizona; and along multiple mesa shelves in Zuni, New Mexico (Bradley, 1973; Evans, et al., 2005; Ferguson, 1996; Tanner, 1958). These locations are often hidden in pocket land areas or deep in canyons with few access trails. Common characteristics of these locations are co-location with runoff catchment from mesa tops, or natural waterways including springs and rivers (Ferguson, 1996; Forde, 1931; Hill, 1938; Pawluk, 1995). Other locations included Pueblo tribal settlements along the Rio Grande River.

Due to the historic practice of seed propa-

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gation, and the geographical isolation of these locations, the resulting populations are likely genetically distinct and could have important horticultural traits such as drought and heat tolerance. A genome-wide analysis of peach germplasm was the focus of several recent studies (Bouhadida et al., 2011; Font et al., 2013; Li et al., 2013; Micheletti et al., 2015) but selections from the North American Southwest (NAS) were not included. Material from these isolated populations might have unique value for modern peach cultivar breeding due to its generations of isolation and inbreeding. Here we report population structure and genetic characteristics of 35 accessions from three isolated peach orchards in three locations representing both Navajo and Hopi tribal lands. The characteristics of orchard sites and population diversity within these orchards and their relationship with modern peach germplasm is discussed.

Materials and Methods

Peach germplasm was collected in three regions representing both Navajo and Hopi tribal lands, with multiple orchards identified in each region: Canyon del Muerto, AZ (CDM1 and CDM2) (21 samples) within Canyon de Chelly National Monument; Jayi Canyon (8 samples) near Navajo Mountain, AZ (NMT1); and Hopi Second Mesa (HTM2; 7 samples) and Third Mesa in AZ (HTM3 and HTM4; 4 samples) (Table 1; *Wytsalucy, 2019*). Samples are defined as a single seed propagated from a single tree from individual orchards with less than 10 trees, except for NMT1 orchard which has near 50 peach trees. Individual samples are labeled by location followed by tree number (eg. NMT101). Collected NAS peach seed were germinated in greenhouses at Utah State University and transplanted after one growing season to a research orchard in Box Elder County, UT. Young actively growing leaf tissue was collected from 40 accessions, freeze-dried and sent to Clemson University for DNA extraction and genotyping. In addition, 20 accessions housed at the *Prunus* National Clonal Germplasm Repository (NCGR) in Davis, CA representing modern and heirloom cultivars and landraces predominantly from the U.S. were included in the diversity study (Table 2). The NCGR accessions were selected to represent a profile of geographical trade market in the United States as well as landraces from Central America and China to aid in origin and diversity studies.

Genomic DNA extraction, library preparation for Genotyping By Sequencing (GBS; Elshire, et al. 2011), and identification of single nucleotide polymorphism (SNP) markers in NAS and NCGR material followed protocols explained in Bielenberg et al. (2015) using the peach genome v2 (Verde, et al. 2017) as the reference genome (RG). Population structure and SNP diversity analyses followed methods reported in Michelleti et al. (2015). Filtering for missing genotype

Table 1. Native American peach orchard locations where seed samples were collected. Locations include Canyon del Muerto, AZ (CDM1-2); Jayi canyon near Navajo Mountain, UT (NMT1); Second and Third Mesas in Hopi, AZ (HTM2-4).

			Site Elevation	Soil*				Water Source Elevation
Location	*n*	Latitude	(m)	pH	EC (dS/m)	Texture	Ann. Precip. (cm)**	(m)***
CDM1	10	36° 09'	1750	7.8	1.0	Sand	23.1	1748St, Wt
CDM2	11	36° 09'	1728	7.8	1.0	Sandy loam	23.1	1725St, Wt
NMT1	11	36° 50'	1356	7.6	0.2	Sand	29.7	1369S, 1346St
HTM2	7	35° 50'	1931	7.9	1.0	Sandy loam	33.0	1931R
HTM3	3	35° 55'	1938	7.9	1.0	Sandy loam	33.0	We
HTM4	1	35° 52'	1740	7.9	1.0	Sand	33.0	1737-1806R

*Source: USDA-NRCS Soil Survey

**Source: weather.gov

***Water Source Key (Sp= Spring; St= Stream; Wt= Watertable; We= Well; R= Surface Runon) rates per accession (--mind 0.25) and per SNP (--geno 0.1), for minor allele frequency (MAF>0.05), and linkage disequilibrium (--indep-pairwise 50000 50 0.8) was done in PLINK (version 1.90b6.9; Chang et al., 2015). The filtered dataset was used to calculate identity-by-descent (--genome), create a distance matrix (--distance square 1-ibs), and run principle components analysis (PCA; --pca), Hardy-Weinberg equilibrium (--hardy) analysis and inbreeding (--het) analysis, also in PLINK. Observed (H_o) and expected (H_e) heterozygosity, and the inbreeding coefficient [F coefficient = ($H_o - H_e$) / $H_T - H_o$)), where H_T = total observations] were calculated for each accession separately. The H_o, H_e, and F coefficient for the NAS selections were also combined independently from modern accessions by summing the counts from the PLINK output. In addition, a Bayesian cluster analysis was done using fastSTRUCTURE (Raj, et al., 2014) with *K* = 2-12 and default parameters to identify *K* subgroups of individuals. Results from fastSTRUCTURE were plotted in R (version 3.5.3) as well as a UPGMA phylogenetic tree from the PLINK distance matrix using the aboot function of the poppr package (version 2.8.1; Kamvar, et al., 2014) to distinguish clustered populations. The reference genome (RG), double haploid of 'Lovell,' was kept in all analyses to observe correlation with NAS samples.

Results and Discussion

A final dataset of 55 accessions (from 60), and 2,042 SNPs (from 22,300) was obtained after filtering. Due to a low genotyping coverage samples NMT102 and CDM102, 203, 205, and 208 were filtered out of the dataset. The mean observed heterozygosity (H_o) for

Table 2. Peach accessions used for comparison to Native American Southwest peaches, including name and their Prunus (PRU) National Clonal Germplasm Repository identifier number (DPRU #), origin and pedigree information where available. OP indicates open pollinated.

Accessions	DPRU #	Origin*	Type (released)*
J.H. Hale	3058	CT, USA	Heirloom (1912)
Red Top	2775	CA, USA	Cultivar (1961)
Elberta	3069	GA, USA	Heirloom (1889)
Chinese Cling	505	China	Heirloom (1850)
Aguascalientes 6-10	676	Mexico	N/A
KIANG-SI	737	Spain	N/A
Yumyeong	1612	South Korea	Cultivar (1977)
Cascata	2007	Brazil	Cultivar (N/A)
Mountain Rose	2163	NJ, USA	Heirloom (1851)
Raritan Rose	2171	CA, USA	Cultivar (1936)
DPRU.520.0003A	520	AZ, USA	N/A
Late Crawford	943	CA, USA	Heirloom (1810)
Boston Red	2141	CA, USA	Cultivar (1959)
Lola Queen	2159	CA, USA	Cultivar (N/A)
Orange Cling	2166	CA, USA	Heirloom (1820)
Stanwick	1132	Syria	Landrace (1843)
Golden Queen Improved	1576	New Zealand	Landrace
Cardinal	3059	GA, USA	Cultivar (1951)
Indian Blood Cling	2151	CA, USA	Landrace likely of Blood Clingstone of France
Springtime	2180	CA, USA	Cultivar (1953)

*Source: USDA-ARS. 2019. GRIN-Global at www.ars-grin.gov/npgs/gringlobal/sb/home.html and Okie, W.R., 1998 modern cultivars and landraces was 0.35, ranging from 0.23 to 0.50, and 0.25 for NAS accessions excluding all HTM3 (HTM301-HTM303) and HTM207 genotypes with a range of 0.21 to 0.32 (Table 3). The mean expected heterozygosity (H_e) for modern accessions was 0.33 and for NAS without HTM30-303 and HTM207 was 0.33. The mean F coefficient for genotypes HTM301-303 was -0.32 and 0.13 for HTM207. The mean average F coefficient for modern accessions was -0.06, ranging from -0.52-0.31 and for NAS was 0.24, ranging from 0.03 to 0.35. The average H_o in modern accessions was similar to the H_o reported for Occidental peach population, but lower in the NAS

Table 3. Genetic diversity estimations for 20 modern accessions and 35 Native American Southwest (NAS) peaches. The five populations suggested by fastSTRUCTURE were Second Mesa in Hopi, AZ (HTM2), Canyon del Muerto, AZ (CDM1-2); Jayi canyon near Navajo Mountain, UT (NMT1), two populations formed by modern accession (Population 1 and 2; including HTM301-303), and eight admixed accessions. A_o = Observed alleles, H_o = Observed heterozygosity; H_e = Expected heterozygosity; F = Write's fixation index.

Sample Name	Population	A_o	H_o	H_e	F
J.H. Hale	Population 1	1116	0.425	0.330	-0.288
Red Top	Population 1	1178	0.400	0.331	-0.207
Elberta	Population 1	973	0.505	0.332	-0.522
Chinese Cling	Population 1	1246	0.352	0.332	-0.059
Aquascalientes 6-10	Population 1	967	0.495	0.333	-0.485
KIANG-SI	Population 1	1206	0.378	0.332	-0.140
Yumyeong	Population 1	1208	0.376	0.331	-0.137
Cascata	Population 1	1335	0.338	0.331	-0.020
Mountain Rose	Population 1	1256	0.356	0.332	-0.073
Raritan Rose	Population 1	1221	0.374	0.332	-0.125
DPRU.520.0003A	Population 2	1375	0.307	0.331	0.074
Late Crawford	Population 2	1412	0.284	0.331	0.143
Boston Red	Population 2	1533	0.230	0.331	0.306
Lola Queen	Population 2	1177	0.395	0.331	-0.194
Orange Cling	Population 2	1459	0.259	0.331	0.218
Stanwick	Admixed	1403	0.277	0.332	0.166
Golden Queen Improved	Admixed	1259	0.348	0.332	-0.047
Cardinal	Admixed	1332	0.319	0.331	0.033
Indian Blood	Admixed	1486	0.236	0.331	0.287
Springtime	Admixed	1189	0.391	0.332	-0.179
HTM401	Admixed	1482	0.253	0.331	0.237
CDM211	Admixed	1543	0.214	0.331	0.354
HTM207	Admixed	1441	0.285	0.331	0.138
CDM101	CDM1	1499	0.239	0.331	0.279
CDM103	CDM1	1516	0.234	0.330	0.291
CDM104	CDM1	1520	0.238	0.331	0.282
CDM105	CDM1	1507	0.253	0.331	0.235
CDM106	CDM1	1512	0.253	0.332	0.238
CDM107	CDM1	1463	0.283	0.331	0.146
CDM108	CDM1	1563	0.214	0.331	0.354
CDM109	CDM1	1385	0.321	0.331	0.030
CDM110	CDM1	1530	0.229	0.331	0.308
CDM201	CDM2	1533	0.236	0.330	0.286

CDM202	CDM2	1484	0.272	0.331	0.178
CDM204	CDM2	1495	0.241	0.331	0.273
CDM206	CDM2	1503	0.256	0.331	0.228
CDM207	CDM2	1518	0.238	0.330	0.279
CDM209	CDM2	1545	0.226	0.331	0.317
CDM210	CDM2	1552	0.215	0.331	0.349
HTM301	Population 1	1142	0.430	0.330	-0.301
HTM302	Population 1	1026	0.490	0.330	-0.483
HTM303	Population 1	1238	0.386	0.330	-0.169
NMT101	NMT1	1513	0.239	0.330	0.277
NMT103	NMT1	1475	0.262	0.332	0.209
NMT105	NMT1	1509	0.237	0.330	0.282
NMT108	NMT1	1441	0.288	0.331	0.130
NMT109	NMT1	1524	0.239	0.331	0.279
NMT111	NMT1	1436	0.296	0.331	0.107
NMT104	NMT1	1466	0.280	0.331	0.155
HTM201	HTM2	1482	0.272	0.331	0.179
HTM202	HTM2	1515	0.219	0.330	0.336
HTM203	HTM2	1518	0.238	0.331	0.282
HTM204	HTM2	1496	0.247	0.331	0.253
HTM205	HTM2	1487	0.270	0.331	0.185
HTM206	HTM2	1471	0.273	0.331	0.174

population (Li et al., 2013; Michelleti et al., 2015). Lower observed heterozygosity in NAS is reflecting their geographical isolation and years of inbreeding.

A UPGMA phylogenetic tree with the 35 Navajo and Hopi genotypes and 20 modern accessions (Fig. 1 A) clearly distinguished two main populations, consisting of NAS genotypes (A), and all modern accessions but including four Hopi genotypes (HTM301-303 and HTM207) (B). The NAS was further clustered into two subgroups, A1, consisting only of Canyon del Muerto (CDM1-2) accessions, and A2, which is further subdivided into two additional subgroups (A2.1 and A2.2). All accessions from Jayi Canyon near Navajo Mountain (NMT1) and one Third Mesa Hopi, AZ accession (HTM401) made up A2.1. A2.2 consists of accessions from Second Mesa in Hopi, AZ (HTM2). Similar clustering was obtained with the PCA and fastSTRUCTURE, confirming 5 distinct subgroups of the peach germplasm (Fig. 1B; PCA data not shown). The five populations suggested by fastSTRUCTURE were HTM2, CDM1-2, NMT1, and two populations formed by the NCGR accessions. Three NAS accessions, HTM301, -302 and -303 grouped with NCGR material and eight accessions were admixed (HTM207, HTM401, CDM211, 'Cardinal', 'Stanwick'. 'Golden Queen Improved', 'Indian blood' and 'Springtime').

Peaches are naturally self-pollinated and can easily develop inbreed populations (99.9% homozygous) after only 6 generations from a single founder individual and more than 10 generations for populations with more than 50 individuals, based on allele frequency (Robertson, 1961). In this study, the NAS population structure depicted extensive inbreeding forming subpopulations different not only from modern accessions but also from those in different regions across the Southwest (Fig. 1). This seems to be the case with a majority of the NAS genotypes since their inbreeding coefficient (F) is 0.24 and they do not cluster with the more heterozygous accessions included in this analysis. The HTM301-303 and HTM207

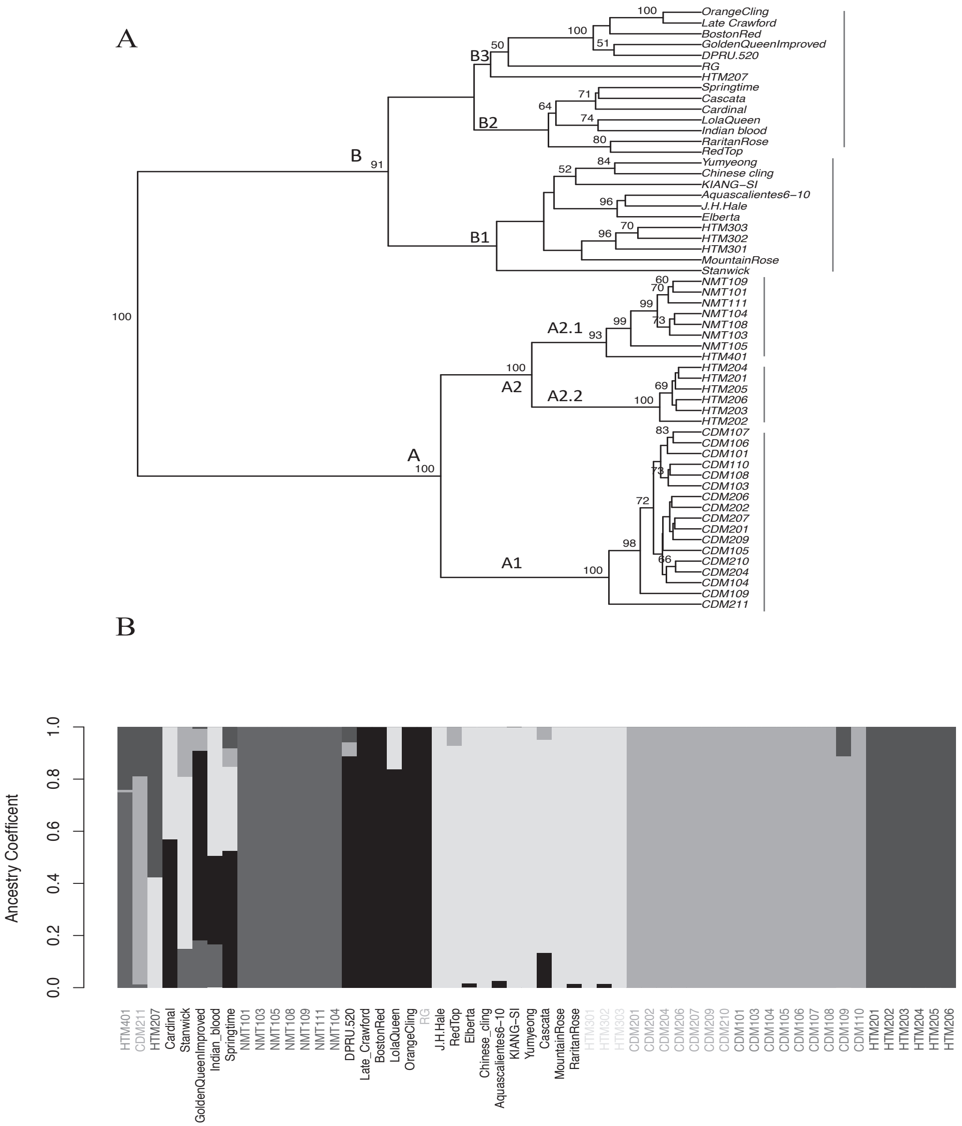

Figure 1. UPGMA tree (A) and clustering by fastSTRUCTURE (*K*=5) (B) for 20 accessions, and 35 North American Southwest (NAS) peach genotypes. NAS accession are listed by location (ex. NMT101) and tree number within location; CDM – Canyon del Muerto; NMT1 – Jayi Canyon near Navajo Mountain, UT; HTM – Hopi Second and Third Mesa, AZ; RG – reference genome. Different shades in panel B indicate groupings from PCA analysis (data not shown).

genotypes grouping with the heterozygous accessions are assumed to be a result of outcrossing with modern cultivars planted sporadically throughout the Hopi communities neighboring the original peach orchards, which began in the late nineteenth century (Diamond, 2010).

The NMT1 population has been completely isolated from modern cultivars as the current caretakers are Navajo elders that continue traditional management practices (Fig. 1B). Dendrochronology methods determined that the current generation of orchard trees at NMT1 are over 80 years old with additional orchard locations near the NMT1 location reflecting the same age span (Wytsalucy, 2019). Both CDM populations are no longer isolated from modern cultivars as nursery material is made available for Navajo youth to rehabilitate their ancestral orchards. The caretakers of both CDM populations continue to practice traditional agriculture and intend to keep their original family seed isolated from modern cultivars.

Conclusion

The inbred NAS populations are particularly isolated and were historically seed propagated, likely resulting in selection pressure for unique horticultural characteristics, such as adaptation to heat and drought. Recent research determined that NMT1 seedlings showed a greater level of drought stress tolerance compared to ‘Lovell’ seedlings, particularly in the rate of recovery from periods of drought stress (Wheeler et al., 2019). Based on the inbreeding estimates of 6 generations (assuming a single founder individual), and dendrochronology analysis indicating that the current generation of trees are more than 80 years old (Wytsalucy, 2019), the isolation period could range from 240-480 years. However, with orchards grown in proximity to modern replants the probability of outcrossing dramatically increases, as has been noted to occur with four of the Hopi samples. Additional work is needed to fully characterize the NAS germplasm in their isolated populations and to preserve this important resource from further genetic contamination.

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About The Cover:

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