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**Economic Botany**

ISSN 0013-0001

Econ Bot

DOI 10.1007/s12231-020-09511-2



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# Characterizing the Diversity of Hawai'i Sweet Potatoes (*Ipomoea batatas* [L.] Lam.)

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Sweet potato (*Ipomoea batatas* [L.] Lam.) is one of the most important staple crops globally with particular cultural and economic significance in the Hawaiian Islands, yet the extent to which traditional cultivars persist remains unknown. The objective of this study was to elucidate the relationships between traditional Hawaiian sweet potato varieties and cultivars that originated elsewhere in the world. We sought to characterize genetic and phenotypic diversity of sweet potatoes represented in the Hawaiian Islands. To this end, a genetic assignment analysis was conducted on a sample of 77 individuals that consisted of traditional Hawaiian, USDA NPGS accessions, and recent herbarium samples. Additionally, voucher specimens of Hawaiian cultivars from the early twentieth century were assessed for variation in leaf morphology. We identified several inconsistencies within the Hawaiian-named varieties, as identically named varieties turned out to be genetically distinct, and similarly named voucher specimens varied in leaf morphology. Our findings call attention to the value of a set of Hawaiian sweet potatoes as “heirloom.” These genetically distinct traditional cultivars have unique value in local markets and present an opportunity to increase cultivar diversity in the markets and fields, support farmer income and diversified agriculture, all while contributing to reinvigoration of Hawaiian cultural heritage.

**Key Words:** Genetic assignment, Leaf shape, Ethnographic records, Botanical garden, Herbarium, Heirloom.

“He ‘uala ka ‘ai ho‘ōla koke i ka wī”,  
The sweet potato is the food that ends  
famine quickly.

-‘Ōlelo no‘eau (Pukui 1983)

## Introduction

Sweet potato (*Ipomoea batatas* [L.] Lam., ‘uala in Hawaiian) is a member of the plant family Convolvulaceae and is an important crop worldwide, with more than 105 million metric tons produced yearly (CIP, n.d.). Sweet potato originated in a region spanning Central and South America, where it diverged from its closest wild relative *I. trifida* - 800,000 years before present (Yang

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Elizabeth Winnicki and Aurora Kagawa-Viviani contributed equally to this work.

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<sup>1</sup>Received 3 February 2020; accepted 3 December 2020; published online \_\_\_\_\_

et al. 2017), followed by multiple hybridization events with *I. triloba* to form the hexaploid *I. batatas* (Muñoz-Rodríguez et al. 2018). From there, the crop found its way to all parts of the world including the Hawaiian archipelago. The most well-supported explanation for its dispersal across Oceania is the “tripartite hypothesis” (Barrau 1957; Green 2005; Yen 1974), which posits that an early *Kumara* sweet potato line was transferred from the South American coast (Scaglione 2005) to central Polynesia around 1000–1100 C.E. and diffused outward with Polynesian voyagers (Athens et al. 2014). Recent findings by Ioannidis et al. (2020) of native South American gene flow into Polynesia around this time provide added support for this exchange of people and plants. Two other lines were transported ~1500 C.E. by Spanish and Portuguese traders, the *Camote* line from Mesoamerica and the *Batata* line from the Caribbean. The geographical patterning suggested by this hypothesis is supported by genetic analysis of extant global collections (Roullier et al. 2013). For the Hawaiian Islands, the earliest archeological record of sweet potato dates to the fourteenth century C.E. in the rain-fed Kohala Field System (Ladefoged et al. 2005), where it served as the key staple in the large dryland field systems of both Hawai‘i Island and Maui (Coil and Kirch 2005; Kirch et al. 2009; Vitousek et al. 2004) and supported populations in arid and coastal areas across the archipelago (Handy 1940).

Tremendous crop diversity is suggested by the ~300 documented Hawaiian names for sweet potato cultivars, suggesting the development of numerous locally-adapted cultivars (Handy 1940; Kagawa-Viviani 2016). This diversity also includes European introductions of sweet potato cultivars new to Hawai‘i, which likely started arriving shortly after Cook’s 1778 arrival (Nagata 1985). By the time the first extensive lists and descriptions were printed ~80 years later (e.g., Kaaie 1860; Napihelua 1857; Rooke 1855), introduced cultivars were already established. Old varieties continued to be valued for medicine and ceremony (Fornander 1919; Kaaikamanu and Akina 1922), but recognition of the loss of ethnobotanical knowledge motivated collections in the early twentieth century (Handy 1940). The twentieth century also saw an acceleration of foreign introductions, breeding, and clonal selection of both natural and artificial sports to support commercial sweet potato production (Chung 1923; Poole 1952, 1955a, 1955b, 1959; Takahashi 1937). We currently know little about the extent to which traditional varieties still persist

across the Hawaiian Islands. At present, more than 30 accessions identified as traditional cultivars are maintained across a half dozen conservation-oriented botanical collections on the islands of O‘ahu, Maui, and Hawai‘i. We use the term “traditional” in this text as a synonym for “heirloom” and “heritage.” We reserve the term “Hawaiian” or “traditional Hawaiian” for cultivars we assume were developed and named by indigenous Hawaiian farmers from germplasm present in the islands prior to 1778, and we use “Hawai‘i” for cultivars presently found in the islands, regardless of origin.

To address this gap in knowledge, nuclear and chloroplast markers were utilized to analyze the genetic diversity among Hawai‘i, USDA NPGS accessions, and herbarium samples. The chloroplast genome encodes a variety of organelle-specific components and is highly conserved (Jansen et al. 2005). As a result, intracellular genetic markers can help illuminate complex evolutionary dynamics and reveal phylogenetic relationships in sweet potato through chloroplast loci analysis (Roullier et al. 2011; Wang et al. 2019; Yan et al. 2015). Additionally, single nucleotide polymorphism (SNP) markers have exceptional utility in many genetic applications, including germplasm characterization which encompasses population structure, genetic diversity and relationships (Ertiro et al. 2015). The diversity of sweet potato can thus be identified based upon SNP genotyping and phylogenetic relation analysis (Feng et al. 2018).

We also evaluated phenotypic diversity among traditional Hawaiian sweet potato cultivars by quantifying leaf morphology from herbarium voucher specimens collected in the early 1900s from Hawaiian farmers across the archipelago in an ethnobotanical survey. Although vine-type plants are known to demonstrate morphological variation throughout their development (heteroblasty) (Lee and Richards 1991), this has not been documented for *Ipomoea batatas*. Instead, Gupta et al. (2020) and Jackson et al. (2020) [and references therein] established that variation in sweet potato leaf morphology is driven by genetics, the growing environment, or both. While our use of herbarium voucher specimens did not allow us to control for either age or environment as in Gupta et al. (2020) and Jackson et al. (2020), the voucher specimens we analyzed provide an important snapshot of diversity.

Renewed interest in traditional cultivars has spurred efforts to bring indigenous crops and cultivars to commercial markets, in large part due to a

potential 400% price premium (Oberholtzer et al. 2005). Indigenous cultural and language resurgence and in-situ conservation motivate recovery of these crops not only for the sake of preserving germplasm, but also to preserve names and stories. In turn, these reflect intrinsic value of traditional cultivars for consumers, adding value for growers.

Sweet potato germplasm present in Hawai'i today is a confusing array of ancient cultivars, introductions from over 200 years of transfers, and an unknown degree of hybridization. Yet clarification and confidence in the identification of traditional cultivars can lead to improved production and value for local producers and practitioners (Kagawa-Viviani et al. 2018). The considerable work already done in another culturally important crop, taro (Helmkamp et al. 2017), largely aligns with traditional groupings. In this study, we sought to elucidate relationships among extant genotypes and historic collections by examining available genetic, phenotypic, and ethnographic data on sweet potato in Hawai'i.

## Materials and Methods

### PLANT MATERIAL

*Ipomoea batatas* DNA was obtained from various repositories: fresh plant tissues from gardens, markets, and collections across the Hawaiian Islands, germplasm originally sourced from the United States Department of Agriculture National Plant Germplasm System (USDA-NPGS), DNA sourced from a Hawaiian plant DNA library (Randell and Morden 1999), and herbarium voucher specimens. The fresh Hawai'i samples included putatively Hawaiian traditional varieties maintained as botanical collections at Waimea Valley Arboretum (O'ahu), UH Mānoa's Harold L. Lyon Arboretum (O'ahu), and Amy Greenwell Ethnobotanical Garden (Hawai'i Island, also represented in the DNA library) and several local varieties from markets on O'ahu. USDA-NPGS germplasm maintained in local facilities represented broad geographic diversity with varieties originating from the Americas, Asia, and Oceania/Indo-Pacific. Finally, pressed tissue samples from the UH Mānoa Joseph F. Rock Herbarium included *I. batatas* from Chinatown markets (downtown Honolulu, O'ahu), Vietnam, and several Pacific Island groups. For a list of all samples see Electronic Supplementary Material [ESM], Appendix 1. DNA from fresh material was extracted with

the DNeasy Plant Mini Kit (Qiagen, Valencia, California) and DNA from herbarium material with the QIAamp DNA Stool Mini Kit (Qiagen, Valencia, California).

### CHLOROPLAST LOCI SAMPLING: HAWAII ACCESSIONS

DNA was obtained from 50 *I. batatas* samples including fresh plant tissues (28 Hawai'i botanical gardens), DNA library (9, Amy Greenwell Ethnobotanical Garden), and dried material (13, UHM Joseph F. Rock Herbarium). For each of these 50 samples (see ESM, Appendix 1), two phylogenetically informative standard chloroplast loci (Graham and Olmstead 2000) *trnL-trnF* and *ycf4* were amplified using PCR with primers designed using Geneious software (Kearse et al. 2012). The subsequent PCR products were sequenced on an ABI 3730 (Applied Biosystems, Foster City, California, USA) and aligned using Geneious software. The *trnL-trnF* and *ycf4* sequences were used to develop phylogenetic trees through two approaches: 1) maximum likelihood phylogeny with the generalized time-reversible (GTR) substitution model (Tavaré 1986), and 1000 bootstrap replications and a transition/transversion rate of four using PhyML 3.0 (Guindon et al. 2010); and 2) Bayesian phylogeny using MrBayes version 3.2.6 (Huelsenbeck and Ronquist 2001) using a GTR substitution model with *Ipomoea indica* as the outgroup. For this, we used the following specifications: gamma rate variation with four categories, Markov Chain Monte Carlo (MCMC) chain length of 100,000 using four heated chains with a subsampling frequency of 500 and burn-in length of 10,000, and a starting random seed of 26,695 with an unconstrained branch length prior. Tree topologies of the two methods were compared for concordance.

### NUCLEAR LOCI SAMPLING: HAWAII AND USDA ACCESSIONS

We analyzed nuclear genomic variation for 77 sweet potato samples representing both local and global diversity. Material was sourced from Hawai'i botanical gardens (29), other local gardens and markets (10), the USDA-NPGS (30), and the UH Mānoa Joseph F. Rock Herbarium (8) (see ESM, Appendix 1). Following extraction, DNA was sent to Rapid Genomics (Gainesville, Florida, USA) for sequencing. Target probe regions were designed for 152 genes which were subsequently sequenced for



each of the 77 samples and analyzed through a standard bioinformatics pipeline. To clean sequences, the 3' end was trimmed by removing low quality bases (quality score < 20). Reads were discarded when more than 10% of the read had a quality score of less than 20. Cleaned reads were aligned with MOSAIK, and FreeBayes (Garrison and Marth 2012) was used for identification of SNPs. Raw VCF and Filter1 VCF with vcftools (Danecek et al. 2011) were general using Filter 1: minQ 10, max-missing-count 3, min-alleles 2, max-alleles 2, min-meanDP 3, max-meanDP 750, maf 0.01, mac 1). This resulted in 27,195 SNP markers.

Genetic assignment was conducted on the sweet potato samples. First, a principal component analysis (PCA) was performed using SNPrelate (Zheng et al. 2012). Next, a discriminant analysis of principal components (DAPC) was conducted using the *adegenet* package in R (Jombart 2008; Jombart and Ahmed 2011), where genetic groups (K) of 2–6 were tested. Based on genetic distance, individuals were considered clones if they were 97% identical. This value was empirically derived by using individuals sourced from different places with the same names (ESM, Appendix 2).

#### HAWAIIAN 'UALA VOUCHER SPECIMENS: LEAF SHAPE, NAMING, AND GEOGRAPHY

We analyzed leaf morphology of 128 pressed voucher specimens of Hawaiian 'uala (sweet potato) housed in the Bernice Pauahi Bishop Museum Herbarium (Honolulu, Hawai'i). Most of the samples were collected between 1912 and 1931 from Hawaiian farmers on the islands of Ni'ihau, O'ahu, Moloka'i, Maui, and Hawai'i. Digital photographs of the voucher specimens were analyzed in ImageJ (Abràmoff et al. 2004; Schneider et al. 2012). For each sample, a single representative leaf was selected and evaluated for leaf area, perimeter, length from petiole to tip, width at widest point, leaf lobe count, and leaf shape following the definitions in *Descriptors for Sweet Potato* (Huamán, 1991, p. 56, Figs. 2 & 3). We derived aspect ratio as length:width and circularity as  $4\pi \times \text{area} / \text{perimeter}^2$  based on their usefulness for capturing variation in *I. batatas* leaf shape (Gupta et al. 2020; Rosero et al. 2019).

We note that Gupta et al. (2020) and Jackson et al. (2020) controlled for both the possibility of heteroblasty (ontogenetic effects) and phenotypic plasticity (environmental effects) on leaf morphology by sampling foliar material at comparable stages of growth under common garden conditions.

Because we could not control for either age or environment with the voucher specimens, we prioritized aspect ratio and circularity as they are less sensitive to environmental influences. We make the necessary assumption that the voucher specimens were sampled from mature, healthy, and representative plants grown under the typical high light conditions ideal for sweet potato cultivation. We, in turn, analyzed undamaged, mature, and representative leaves from each voucher specimen.

To better understand the connection between varietal names and phenotypes, we focused on a subset of traditional Hawaiian sweet potato names. Varieties or variety clusters associated with the name *Mohihi*, *Huamoa*, and *Piko* are relatively well described in written records from the past century (Kagawa-Viviani 2016) and were represented by multiple herbarium voucher specimens. We examined leaf morphology and sampling locales to better understand associations between names, phenotypes, and geographic distribution of these once popular varieties.

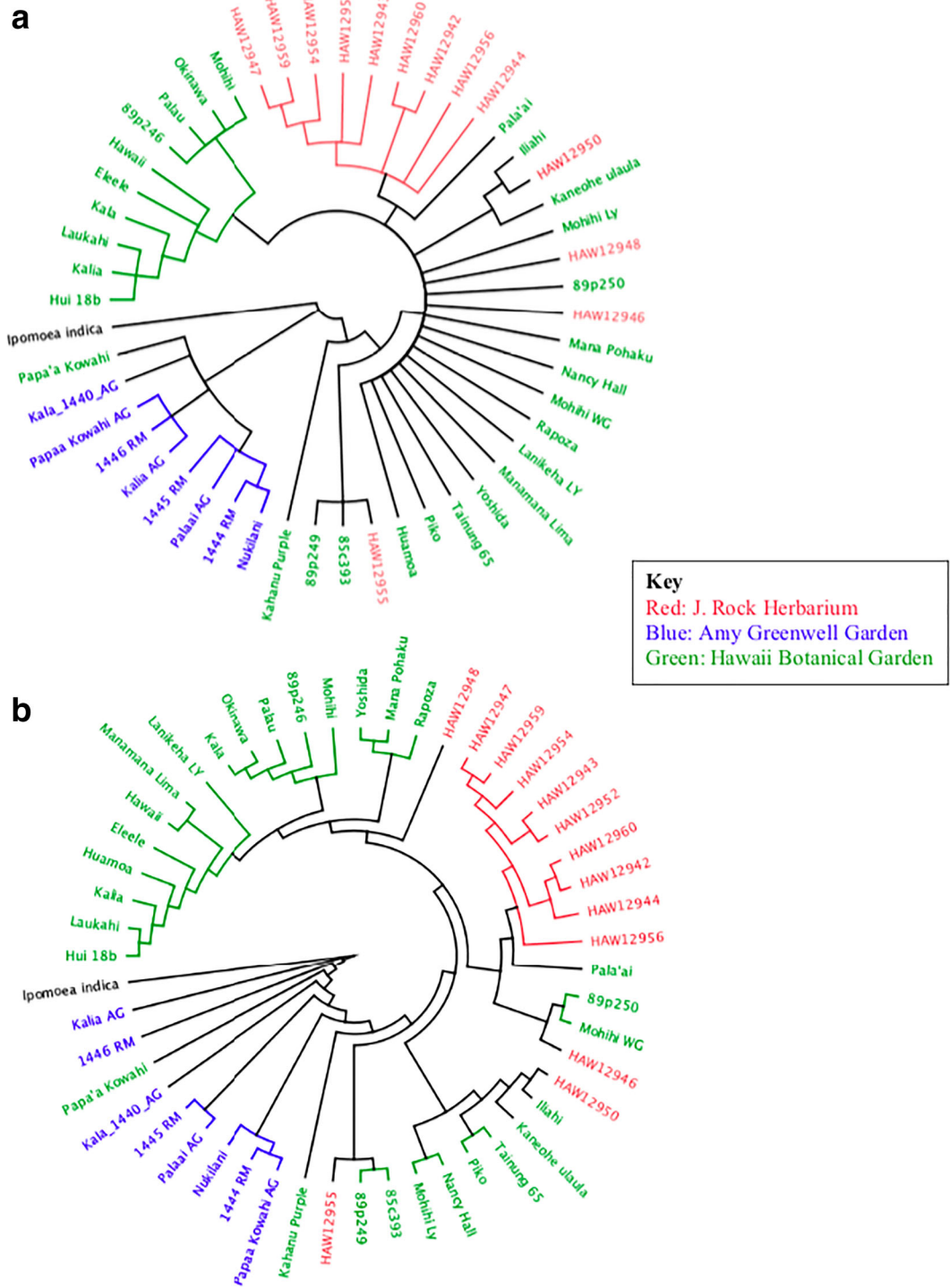
## Results

### CHLOROPLAST LOCI-BASED ANALYSES

The results of our chloroplast loci (trnL-trnF and ycf4) analysis indicate strong separation of the Hawai'i (fresh tissue) samples from UHM Joseph Rock Herbarium samples representing *I. batatas* collected outside of Hawai'i, regardless of the method used for tree construction (ML or Bayesian). Furthermore, cultivars from Amy Greenwell Ethnobotanical Garden (Kona, Hawai'i) formed a cluster distinct from cultivars from all other Hawai'i botanical gardens (Fig. 1). While purportedly traditional Hawaiian varieties *Kala*, *Kalia*, and *Pala'ai* sourced from fresh tissues and the Amy Greenwell DNA library samples were separated on both trees, the analysis suggests consistency for *Papa'a kowahi*, where fresh tissue indicate similarity to the older accession from Amy Greenwell.

### NUCLEAR LOCI ANALYSES

Clear sub-populations emerged at K = 3, 4, 5, and 6 clusters within our samples of *I. batatas* (Fig. 2). At K = 3, cluster 1 (purple) included varieties from Hawai'i gardens and markets: the purple-fleshed, white-skinned *Rapoza*, *Iliahi*, and *Ogasawara*, the undescribed *Ko'oko'au* [sic] and



**Fig. 1.** Reconstruction of chloroplast trnL-trnF-ycf4 phylogeny using A) Bayesian and B) maximum likelihood methods.

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[VOL

K=2	K=3	K=4	K=5	K=6	
					Iliahi (Waimea Garden, Oahu)
					Rapoza (Waimea Garden, Oahu)
					Ogasawara (local farm on Oahu)
					Hui 18b (Hui Ku Maoli Ola nursery, Oahu)
					Ko'oko'au (Urban Garden Center, Oahu)
					HAW12950 (Honolulu, Chinatown)
					HAW12952 (Honolulu, Chinatown)
					USDA_585080: Camote blanco (Guatemala)
					USDA_599368: Cuba 2 (Cuba)
					USDA_573316: Hawaii (Tonga)
					USDA_573330: ACC108 (Solomon Islands)
					USDA_667652: Toni (Fiji)
					USDA_667651: Kuma 2 (Fiji)
					USDA_667649: IB/PNG/39 (Fiji)
					USDA_318846: N.Z. 196 (613) (Indonesia)
					USDA_573309: L329 (Papua New Guinea)
					USDA_573287: Woksaken (LO49) (Papua New...
					HAW12959 (Mariana Islands)
					HAW12953 (Vietnam)
					HAW12954 (Vietnam)
					HAW12955 (Vietnam)
					HAW12956 (Vietnam)
					USDA: Satsuma_2 (unknown)
					Satsuma (Oahu, local market)
					Yama (Oahu, local market)
					Pa'u o Hiriaka (Amy Greenwell Garden, Hawaii)
					Mahina (Oahu, local market)
					Kalila (Lyon Arboretum, Oahu)
					Huamoa_2003.0254 (Lyon Arboretum via AG)
					83c843 (Waimea Garden, Oahu)
					CN 1367-2 (Taiwan)
					Nancy Hall (Waimea Garden, Oahu - from C&C...
					Anunoa (unknown)
					89p250 (Waimea Garden, Oahu)
					Morado (Peru)
					USDA_531094: 392 (Guatemala)
					USDA_634399: Picadito (Cuba)
					USDA_566613: Beauregard (Louisiana, USA)
					Diane (local farm on Maui)
					USDA_666143: L 78-21 (USA)
					USDA_595199: Darby (Louisiana, USA)
					USDA_566627: Georgia Jet (Georgia, USA)
					USDA_566619: Centennial (South Carolina, USA)
					USDA_12_USA: Centennial (South Carolina, USA)
					USDA_634400: Red Resisto (Peru)
					USDA_566651: Resisto (USA)
					USDA_585088: Tainung 66 (Taiwan)
					USDA_667650: Anny (Fiji)
					USDA_674101: Finlay (Fiji)
					Yoshida (Local research collection)
					USDA_566657: Sumor (South Carolina, USA)
					USDA_634398: Pelican Processor (Louisiana)
					USDA_666141: W-390 (South Carolina, USA)
					USDA_599388: Liaoshu 40 (China)
					Kona B (local research collection)
					HAW12944 (Kauai)
					Kala (Lyon Arboretum, Oahu via WG)
					Kala_1440_AG (Amy Greenwell Garden, Hawaii)
					89p249 (Waimea Garden, Oahu)
					89p246 (Waimea Garden, Oahu)
					Huamoa (Lyon Arboretum, Oahu)
					Huamoa_1438 (Amy Greenwell Garden, Hawaii)
					Papa'a Kowahi (Waimea Garden, Oahu)
					Eleele (Waimea Garden, Oahu)
					Lanikeha LY (Lyon Arboretum, Oahu)
					Lanikeha_1 (Waimea Garden, Oahu)
					Piko (Waimea Garden, Oahu)
					Pala'ai (Waimea Garden, Oahu)
					Palau_WaimeaGarden (Waimea Garden, Oahu)
					Palau_LyonArboretum (Lyon Arboretum, Oahu via WG)
					Manamana Lima (Maui Nui Botanical Garden, Maui)
					85c393 (Waimea Garden, Oahu)
					Laukahi (Urban Garden Center, Oahu)
					Mana Pohaku (Lyon Arboretum, Oahu)
					Kane'ohe (Maui Nui Botanical Garden, Maui via WG)
					Okinawa (Urban Garden Center, Oahu)
					Mohihi (Lyon Arboretum, Oahu via WG)



◀ **Fig. 2.** Discriminant analysis of principal components exploring K2–K6 groups, where each column indicates how varieties clustered depending on the number of groups specified. The specific ordering and proximity of two individuals within a cluster is not related to genetic distance. With clustering optimized at K = 3, Hawai'i/USDA/Herbarium varieties, Hawai'i botanical garden varieties, and USDA germplasm varieties grouped together. As group number increased (K = 5 and 6), Hawai'i botanical garden varieties grew increasingly genetically distinct.

*Hui 18b*, and *HAW12952* and *HAW12950* from Honolulu Chinatown. This cluster also included samples sourced from USDA-NPGS: yellow-fleshed *Acc108* from the Solomon Islands, *CUBA 2* from Cuba, and *Camote blanco* from Guatemala. K = 3/cluster 2 (green) included a combination of varieties sourced from USDA-NPGS's more global collection and several locally popular varieties such as the yellow-fleshed *Nancy Hall* and Japanese-type white-fleshed, pink skin varieties (*Yama*, *Satsuma*). This cluster also included several varieties assumed to be Hawaiian (*Pa'ū o Hi'iaka*, *Huamoa*, *Kalia*, *89p250*, *Mahina*) tending to be pale-fleshed from white to cream to yellow. K = 3/cluster 3, on the other hand, was dominated by varieties maintained in Hawai'i botanical gardens (Fig. 2, red).

At K = 4, a fourth grouping emerged from within the K = 3/cluster 2 that consisted almost entirely of USDA-NPGS samples (Fig. 2, blue). Accession records and notes revealed seven of the twelve varieties to be moist, orange-fleshed, red-skinned cultivars developed in the US Southeast (Louisiana, South Carolina, and Georgia) often marketed as "yams." Other varieties included cream-fleshed varieties (*Sumor* from South Carolina and *Hawaii* from Tonga) and two undescribed accessions from Fiji (*Anny* and *Finlay* K = 5, the K = 3/cluster 3 split into two groups, one consisting of suspected local adoptions [*Mana pohaku*, *Okinawa*] and several varieties with the same name assigned to multiple known phenotypes including both white-fleshed and purple-fleshed cultivars [*Mohihi*, *Kaneobe*] (Fig. 2, yellow). Unfortunately, we were unable to confirm the specific phenotypes associated with these samples.

The remainder of this cluster (column 4, red) included what has been documented in ethnographic and botanical garden accession records or suspected by growers to be traditional, "old Hawaiian" varieties. These include the very deep purple fleshed/purple-skinned *Papa'a kowahi* and 'Ele'ele, the light yellow-fleshed/purple-skinned *Kala* and

*Piko*, and the yellow-fleshed/ light-skinned *Huamoa*, *Palā'ai*, *Lanikeha*, and *Manamana lima*. The unnamed varieties *89p246* and *89p249* recovered at a Lāna'i island roadside were also included in this group. We note that this group also included some USDA-NPGS varieties; ones we have descriptions for indicate they are cream to yellow-fleshed. We note that the sixth cluster emerging at K = 6 (orange) are all characterized by varieties with cream to yellow flesh.

We observed in this analysis that multiple samples labeled as *Huamoa* ended up in different clusters at K = 6, even when drawn from the same botanical garden. *Huamoa\_1438* was drawn from a DNA library developed in the 1990s, while *Huamoa\_2003.0254* was sampled at a later date from the same garden, Amy Greenwell Ethnobotanical Garden. *Huamoa* (Lyon) thus appears to be more closely associated with the older accession, and it is possible that collection mix-up could have occurred at Amy Greenwell between the two sampling times.

Reassuringly, a number of identically-named cultivars from different botanical gardens clustered together. Besides *Huamoa* (Amy Greenwell, Lyon), this applied to cultivars labeled as *Kala* (Amy Greenwell, Lyon) and cultivars labeled as *Palau* (Waimea, Lyon) for each K-means 3, 4, 5, and 6. The exception here is for *Lanikeha*, where the samples from Lyon and Waimea clustered into different groups at K = 6, suggesting a need to assess collection fidelity through phenotyping, genotyping, or common garden experiment.

#### ANALYSIS OF HAWAIIAN 'UALA VOUCHER SPECIMENS AND NAMES

In our survey of the 128 voucher specimens housed at the Bishop Museum Herbarium, we observed several names occurred with higher frequency across the Hawaiian Islands. These included *Mohihi*, which was documented as *mohihi a mohaluhalu* (Molokai), *mohihi keokeo* and *mohihi ulaula* (collected at Laupāhoehoe, Hawai'i, as transfers from Waihe'e, Maui), *mohihi keokeo* and *mohihi ulaula* (Kaupō, Maui), or simply *mohihi* (Kona, Hawai'i; Mokulē'ia and Mākiki, Oahu). *Piko* was documented as *piko hao*, *piko manamana*, and *piko nui* (Mokulē'ia, O'ahu). *Huamoa* was *huamoa ulaula* and *huamoa keokeo* (Kaupō, Maui), or simply *huamoa* (Ni'ihau; Mākiki, O'ahu; Kona, Hawai'i). We note that these cultivars sharing common epithets *piko*, *huamoa*, and *mohihi* do not



cultivation of traditional, heirloom Hawaiian sweet potato. We also discuss study limitations and opportunities for future work, including a need to compare extant Hawaiian varieties with the historical collections housed at the Bernice P. Bishop Museum Herbarium.

#### STATUS OF HAWAIIAN SWEET POTATO CULTIVAR DIVERSITY

Our chloroplast and nuclear loci analyses both indicate that many traditional sweet potato varieties maintained in Hawai'i botanical garden collections (ex-situ conservation) are distinct from cultivars sourced from elsewhere in the Pacific region and the world. We do not see evidence of strong widespread admixture, or hybridization, of assumed old Hawaiian cultivars and newer introductions. Furthermore, the distinct clustering of several Amy Greenwell cultivars among those currently grown in Hawai'i in the chloroplast analysis suggests these accessions are exceptional among the botanical gardens. Our nuclear loci analysis confirmed that extant Hawaiian sweet potato genotypes are different from moist, orange-fleshed "yams" of U.S. provenance as well as the locally popular and drier purple-fleshed, white-skinned "Okinawan" types. Some overlap with white-fleshed, pink-skinned Japanese types, however, is apparent. We conclude that distinct sweet potato lineages have been maintained in Hawai'i even through at least a century of introductions and breeding of sweet potatoes, including with old Hawaiian varieties.

As we increased the number of clusters from  $K = 5$  to  $K = 6$ , Hawaiian cultivars separated into two, then three groupings. From these groupings, we infer that more genetic diversity is present among the Hawaiian samples than among herbarium and USDA germplasm samples we evaluated. Hawaii's environmental heterogeneity and pre-contact geopolitical complexity provided a context where native farmers of old might have rapidly developed and maintained distinct varieties fit for local climate, soils, and social preferences. This highlights the importance of maintaining traditional Hawaiian sweet potato diversity and preserving the current gene pool. Our work serves as a step toward identifying the unique alleles present across Hawaiian sweet potatoes that could help present-day farmers better understand and value the diversity of traditional varieties.

#### VARIETAL CONFUSION HIGHLIGHTS NEED TO VERIFY COLLECTIONS AND INVEST IN EX-SITU CONSERVATION

Understanding population genetic structure is a common objective of exploring biodiversity. It is also important when considering conservation and plant breeding. Population structuring occurs when there is a shared history of mutation, migration, selection, and/or drift (Bossart and Prowell 1998; Foll and Gaggiotti 2006; Loveless and Hamrick 1984). Specific phenomena that frequently cause structure in crop plants are mating systems (St. Onge et al. 2011), human use (Taitano et al. 2018), distance between breeding populations (Platt et al. 2010), and environmental gradients that lead to local adaptation within populations (Frichot et al. 2013). Overall levels of diversity can be greatly increased with very little sexual recombination (Roselius et al. 2005). Roullier et al. (2013) identified that the bright yellow color of *Kumara* cultivars was heavily selected but that background was largely heterogeneous. This was due to the mixed clonal/sexual mating system in sweet potato. In our data set, we identified that while this occasionally occurred, more often than not Hawaiian germplasm was more closely related to other Hawaiian material than germplasm sourced from different locations.

The differentiation of the Amy Greenwell Ethnobotanical Garden collection from other Hawai'i botanical gardens in the chloroplast analysis indicates garden-specific differences in Hawaiian sweet potato ex-situ conservation. We suggest that garden's location in fertile remnants of the Kona field system (Kelly 1983), explicit focus on Hawaiian ethnobotany/culturally-relevant plants, staff/community commitment to Hawaiian crop plants, and stable leadership enabled continuity of its Hawaiian 'uala collection through the 1990s construction of the DNA library (Randell and Morden 1999).

Our chloroplast and nuclear loci analyses indicate inconsistencies between identically-named germplasm, highlighting gaps in the conservation of old cultivars. While the similarity between the *Papa'a kowabi* sampled from Amy Greenwell in the 1990s (DNA library) and *Papa'a kowabi* in the current collection indicate successful conservation of this genotype (Fig. 1), the distant placement of *Kala*, *Pala'ai*, and *Kalia* sourced from the DNA library vs. fresh tissues suggest genetic differentiation over time between the 1990s and 2014. Follow-up work is

required to identify the reason: sample or accession mix-up, genetic drift, or hybridization.

Similarly, the nuclear analyses of fresh plant tissues confirmed both redundancy and mix-ups across extant sweet potato collections. In some cases, identically-named samples from different gardens grouped together into the same clusters (redundancies). Mix-ups are implied when such samples fell into different groups, indicating a need to revisit and verify the accessions. Thus, molecular tools are useful for identifying coverage and gaps in 'uala cultivar conservation. We note that collection managers and grounds staff across Hawai'i's conservation-oriented botanical gardens have done tremendous work to collect and preserve Hawaiian crop plants, exchanging planting material and accession records with each other. Yet without an integrated approach for tracking these exchanges and verifying cultivars, important information on a fuller set of Hawaiian 'uala diversity remains fragmented across garden accession records and collection manager memories (T. Sherrill, D. Orr, P. Van Dyke, pers. comm.). Our concern is that cultivars can thus be easily lost without anyone even noticing.

#### PHENOTYPES AND GENOTYPES: OPPORTUNITIES AND CHALLENGES OF HERBARIUM COLLECTIONS

The analysis of Bishop Museum Herbarium voucher specimens indicates that varieties with similar names and collected from the same island are often phenotypically—and we suspect genotypically—distinct. Our comparison of leaf shape and accession notes lead us to conclude that leaf shape does not serve as the central basis for Hawaiian varietal naming and/or some shuffling of names occurred. That said, we acknowledge that sweet potato leaf traits exhibit strong environmental plasticity (Gupta et al. 2020) and mutate even on the same stem (Yen 1963). While we will never be able to fully characterize their phenotypes, these herbarium samples, as the earliest historical collection of Hawaiian sweet potato cultivars, are a crucial resource for assessing their diversity. We were unable to access the Bishop Museum's voucher specimens for DNA analysis nor match samples common to our study and Roullier et al. (2013), but future work should seek to compare historic and current-day collections in terms of both phenotypes and genotypes.

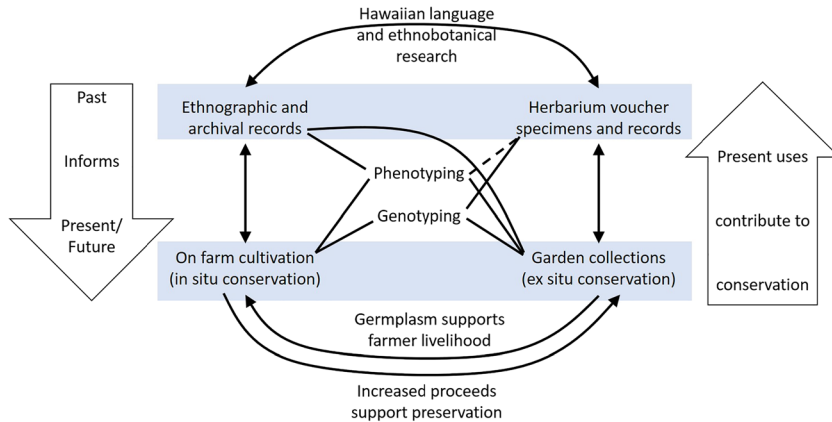
#### TOWARD CONNECTING HISTORICAL AND LIVING COLLECTIONS

Roullier et al. (2013) point out that a multi-pronged approach is required to interpret historic plant movements in light of modern plant movements and recombination. Similarly, a multi-pronged approach is also required to conserve indigenous crop diversity. We suggest a framework for coordinating efforts to comprehensively research, phenotype, and genotype Hawaiian 'uala through time by working with oral traditions to current day farms (Fig. 4) which would help increase understanding, cultivation, and enjoyment of this indigenous crop.

#### IMPLICATIONS FOR IN-SITU CONSERVATION, BREEDING, AND SELECTION OF TRADITIONAL CROPS

By confirming the historic status of cultivars, we suggest farmers and cultural practitioners wanting to perpetuate "heirloom" varieties can add value to their operations. This would incentivize the conservation and active propagation of these museum cultivars for growers and crop biodiversity conservation efforts alike, not only in gardens (ex-situ) but on farm (in-situ). Increasing the profit margin for crops may mitigate risk for farmers growing on smaller land areas. The diversity of sweet potato cultivars currently being maintained in gardens can make their way to tables and increase public awareness of crop biodiversity. Genetic assignment analysis is just one component of an effort to understand the diversity and uniqueness of culturally important crops. Data presented here provide a better understanding of the diversity of distinctly Hawaiian sweet potatoes which could lead to potential for niche production on local farms.

When working with indigenous crops, however, care must be taken to engage indigenous communities to ensure open and equitable communication and address concerns regarding bio-prospecting or misappropriation of culturally important germplasm. In Hawai'i, previous attempts to patent taro (*Colocasia esculenta*) hybrids and explore genetic engineering for disease resistance resulted in public protest, due in part to the fact that the plant is considered an ancestor of the Hawaiian people (Farran 2014; Gugganig 2017). Although sweet potato does not generally hold as important a position as taro in Hawaiian origin stories, it is considered a body form (*kinolau*) of the god Lono, is used



**Fig. 4.** Framework in which ethnographic and archival research, herbarium specimens, conservation-oriented (ethno)botanic gardens and collections, and farmers interested in heirloom cultivars might work more synergistically to collectively reinvigorate Hawaiian ‘uala in current-day economic landscapes. Phenotyping and genotyping Hawaiian cultivars will support in-situ, on-farm cultivation, while the added value from these efforts should contribute to the often financially- strapped operations and staff working in gardens, museums, and archives that maintain the names and histories creating that value.

in medicines and ceremony, and is considered a more important staple than taro in some regions (Handy et al. 1991; Kagawa-Viviani et al. 2018). Scientists should engage with community members to vet their proposed research, ideally a priori, to ensure that communities are not just aware of, but are involved in, consent to and, to the extent possible, drive research that involves cultural resources (Chung-Do et al. 2019; Keaulana et al. 2019).

## Conclusion

The sweet potato varieties present in Hawai‘i represent a diverse array of cultivars. Yet many of the named Hawaiian varieties of sweet potato remain genetically distinct from sweet potato varieties grown in the United States and elsewhere around the world. Our analysis highlighted a need to address naming inconsistencies or record-keeping errors among varieties with Hawaiian names, as identically-named varieties appeared in multiple genetic groupings. Our chloroplast analysis showed that cultivars maintained at the Amy Greenwell Ethnobotanical Garden are genetically distinct, even within the broader pool of Hawaiian sweet potato varieties. These unique genotypes should be maintained and leveraged as certified “heirloom” which may provide added appeal in the markets and incentive to farmers to grow them. At the same time, more effort is needed to elucidate the basis

for differences between genetic clusters. Lastly, leaf morphology of Hawaiian sweet potatoes varies considerably even among varieties carrying the same name, highlighting a gap in our knowledge of naming conventions. Our work demonstrates how integrating genetic, morphological, and ethnographic data can strengthen our understanding of Hawai‘i and Hawaiian sweet potato diversity and contribute to the preservation, historical significance, and vitality of this important crop.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1007/s12231-020-09511-2>.

## Acknowledgments

We thank Jay Bost, Tia Silvasy, and Sarah Moore. We would like to extend our gratitude to the American Society of Plant Biologists National Summer Undergraduate Research Fellowship for supporting EW. AKV would like to acknowledge Penny Levin for mentoring, support, and encouragement to keep on the ‘uala. We also thank those that maintain accessions and who made plant material available—various gardens and growers, herbaria, and the Waimanalo Agricultural Experiment Station. Last but not least, we acknowledge the early motivation for this effort—Anakala Jerry



Konanui's persistent request to untangle Hawaiian 'uala with molecular tools. *Pīpi holo ka' ao*.

### Literature Cited

- Abràmoff, M. D., P. J. Magalhães, and S. J. Ram. 2004. Image processing with ImageJ. *Biophotonics International* 11(7): 36–42.
- Athens, J. S., T. M. Rieth, and T. S. Dye. 2014. A paleoenvironmental and archaeological model-based age estimate for the colonization of Hawai'i. *American Antiquity* 79(1):144–155.
- Barrau, J. 1957. L'énigme de la patate douce en Océanie. *Etudes d'Outre-Mer* 40:83–87.
- Bossart, J. L. and D. P. Prowell. 1998. Genetic estimates of population structure and gene flow: Limitations, lessons and new directions. *Trends in Ecology and Evolution* 13(5): 202–206. [https://doi.org/10.1016/S0169-5347\(97\)01284-6](https://doi.org/10.1016/S0169-5347(97)01284-6).
- CIP [Centro Internacional de la Papa - International Potato Center]. (n.d.). Sweet potato facts and figures. Retrieved from <https://cipotato.org/sweetpotato/sweetpotato-facts-and-figures/>.
- Chung, H. L. 1923. The sweet potato in Hawaii. Hawaii Agricultural Experiment Station Bulletin 50. Honolulu, Hawaii: United States Department of Agriculture Hawaii Agricultural Experiment Station. <http://hdl.handle.net/10125/25538>.
- Chung-Do, J. J., I. Ho-Lastimosa, S. Keaulana, K. Ho Jr., P. W. Hwang, T. Radovich, L. Albinio, I. Rogerson, L. Keli'iholokai, K. Deitschman, and M. S. Spencer. 2019. Waimānalo pono research hui: A community–academic partnership to promote native Hawaiian wellness through culturally grounded and community-driven research and programming. *American Journal of Community Psychology* 64(1–2): 107–117. <https://doi.org/10.1002/ajcp.12355>.
- Coil, J. and P. V. Kirch. 2005. An Ipomoean landscape: Archaeology and the sweet potato in Kahikinui, Maui, Hawaiian Islands. In: *The sweet potato in Oceania: A reappraisal*, eds. C. Ballard, P. Brown, R. M. Bourke, and T. Harwood, 71–84. Sydney, Australia: University of Sydney.
- Danecek, P., A. Auton, G. Abecasis, C. A. Albers, E. Banks, M. A. DePristo, R. E. Handsaker, G. Lunter, G. T. Marth, S. T. Sherry, G. McVean, R. Durbin, and 1000 Genomes Project Analysis Group. 2011. The variant call format and VCFtools. *Bioinformatics* 27(15): 2156–2158. <https://doi.org/10.1093/bioinformatics/btr330>.
- Ertiro, B. T., V. Ogugo, M. Worku, B. Das, M. Olsen, M. Labuschagne, and K. Semagn. 2015. Comparison of Kompetitive Allele Specific PCR (KASP) and genotyping by sequencing (GBS) for quality control analysis in maize. *BMC Genomics* 16: 908. <https://doi.org/10.1186/s12864-015-2180-2>.
- Farran, S. 2014. That plant is my ancestor: Dilemmas for intellectual property in developing countries, food security and Pacific Island countries. *Queen Mary Journal of Intellectual Property* 4(4): 277–296. <https://doi.org/10.4337/qmjip.2014.04.02>.
- Feng, J. Y., M. Li, S. Zhao, C. Zhang, S. T. Yang, S. Qiao, W. F. Tan, H. J. Qu, D. Y. Wang, and Z. G. Pu. 2018. Analysis of evolution and genetic diversity of sweetpotato and its related different polyploidy wild species *I. trifida* using RAD-seq. *BMC Plant Biology* 18: 181. <https://doi.org/10.1186/s12870-018-1399-x>.
- Foll, M. and O. Gaggiotti. 2006. Identifying the environmental factors that determine the genetic structure of populations. *Genetics* 174(2): 875–891. <https://doi.org/10.1534/genetics.106.059451>.
- Fornander, A. 1919. He Moolelo no ka Mahiai. In: *Fornander collection of Hawaiian antiquities and folk-lore*, tran. T. G. Thrum, 161–171. Honolulu, HI: Bishop Museum Press.
- Frichot, E., S. D. Schoville, G. Bouchard, and O. François. 2013. Testing for associations between loci and environmental gradients using latent factor mixed models. *Molecular Biology and Evolution* 30(7): 1687–1699. <https://doi.org/10.1093/molbev/mst063>.
- Garrison, E. and G. T. Marth. 2012. Haplotype-based variant detection from short-read sequencing. arXiv preprint arXiv:1207.3907. <https://arxiv.org/pdf/1207.3907.pdf>.
- Graham, S. W. and R. G. Olmstead. 2000. Utility of 17 chloroplast genes for inferring the phylogeny of the basal angiosperms. *American Journal of Botany* 87(11): 1712–1730. <https://doi.org/10.2307/2656749>.
- Green, R. C. 2005. Sweet potato transfers in Polynesian prehistory. In: *The sweet potato in Oceania: A reappraisal*, 43–62. Sydney, Australia: University of Sydney.
- Gugganig, M. 2017. The ethics of patenting and genetically engineering the relative Hāloa.

- Ethnos 82(1): 44–67. <https://doi.org/10.1080/00141844.2015.1028564>.
- Guindon, S., J. F. Dufayard, V. Lefort, M. Anisimova, W. Hordijk, and O. Gascuel. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology* 59(3): 307–321. <https://doi.org/10.1093/sysbio/syq010>.
- Gupta, S., D. M. Rosenthal, J. R. Stinchcombe, and R. S. Baucom. 2020. The remarkable morphological diversity of leaf shape in sweet potato (*Ipomoea batatas*): The influence of genetics, environment, and GxE. *New Phytologist* 225(5):2183–2195. <https://doi.org/10.1111/nph.16286>.
- Handy, E. S. C. 1940. The Hawaiian planter, Vol. I: His plants, methods and areas of cultivation. Bernice P. Bishop Museum Bulletin 161. Honolulu, Hawaii: Bishop Museum Press.
- Handy, E. G. Handy, and M. K. Pukui. 1991. Native planters in old Hawaii: Their life, lore, and environment. Revised edition. Honolulu, Hawaii: Bishop Museum Press.
- Helmkamp, M., T. K. Wolfgruber, M. R. Bellinger, R. Paudel, M. B. Kantar, S. C. Miyasaka, H. L. Kimball, A. Brown, A. Veillet, A. Read, and M. Shintaku. 2017. Phylogenetic relationships, breeding implications, and cultivation history of Hawaiian taro (*Colocasia esculenta*) through genome-wide SNP genotyping. *Journal of Heredity* 109(3): 272–282. <https://doi.org/10.1093/jhered/esx070>.
- Huamán, Z. 1991. Descriptors for sweet potato. CIP, AVRDC, IBPGR, Rome, Italy.
- Huelsensbeck, J. P. and F. Ronquist 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17(8): 754–755.
- Ioannidis, A. G., J. Blanco-Portillo, K. Sandoval, E. Hagelberg, J. F. Miquel-Poblete, J. V. Moreno-Mayar, J. E. Rodríguez-Rodríguez, C. D. Quinto-Cortés, K. Auckland, T. Parks, K. Robson, A. V. S. Hill, M. C. Avila-Arcos, A. Sockell, J. R. Homburger, G. L. Wojcik, K. C. Barnes, L. Herrera, S. Berríos, M. Acuña, E. Llop, C. Eng, S. Hunsman, E. G. Burchard, C. R. Gignoux, L. Cifuentes, R. A. Verdugo, M. Moraga, A. J. Mentzer, C. D. Bustamante, and A. Moreno-Estrada. 2020. Native American gene flow into Polynesia predating Easter Island settlement. *Nature* 583: 572–577. <https://doi.org/10.1038/s41586-020-2487-2>.
- Jackson, D. M., H. F. Harrison, R. L. Jarret, and P. A. Wadl. 2020. Phenotypic variation in leaf morphology of the USDA, ARS sweetpotato (*Ipomoea batatas*) germplasm collection. *HortScience* 55(4): 465–475. <https://doi.org/10.21273/HORTSCI14703-19>.
- Jansen, R. K., L. A. Raubeson, J. L. Boore, C. W. dePamphilis, T. W. Chumley, R. C. Haberle, S. K. Wyman, A. J. Alverson, R. Peery, S. J. Herman, H. M. Fourcade, J. V. Kuehl, J. R. McNeal, J. Leebens-Mack, and L. Cui. 2005. Methods for obtaining and analyzing whole chloroplast genome sequences. *Methods in enzymology* 395: 348–384. [https://doi.org/10.1016/S0076-6879\(05\)95020-9](https://doi.org/10.1016/S0076-6879(05)95020-9).
- Jombart, T. 2008. adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics* 24(11): 1403–1405. <https://doi.org/10.1093/bioinformatics/btn129>.
- Jombart, T. and I. Ahmed. 2011. adegenet 1.3–1: New tools for the analysis of genome-wide SNP data. *Bioinformatics* 27(21): 3070–3071. <https://doi.org/10.1093/bioinformatics/btr521>.
- Kaaiakamanu, D. M. and J. K. Akina. 1922. Hawaiian herbs of medicinal value. Honolulu: Territory of Hawaii Board of Health.
- Kaai, J. W. K. 1860. Inoa a na Uala. *Ka Hae Hawaii [Hawaii]* 4(52): 205. <http://www.nupepa.org/gsd12.5/cgi-bin/nupepa?e=d-0nupepa%2D%2D00-0-0%2D%2D010%2D%2D-4%2D%2D%2D%2D-text%2D%2D-0-11%2D%2D1haw-Zz-1%2D%2D-20-about%2D%2D-0003-1-0000utfZz-8-00&c=CL2.16&d=HASHd6a2ac7ad98fb43da966a2.3&l=en>.
- Kagawa-Viviani, A. 2016. Untangling ‘uala: Toward re-diversifying and re-placing sweet potato in the Hawaiian landscape. Report submitted to E Kūpaku Ka ‘Āina- The Hawai‘i Land Restoration Institute, Wailuku, Hawai‘i.
- Kagawa-Viviani, P. Levin, E. Johnston, J. Ooka, J. Baker, M. Kantar, and N. K. Lincoln. 2018. I Ke Ēwe ‘Āina o Ke Kupuna: Hawaiian ancestral crops in perspective. *Sustainability* 10(12): 4607. <https://www.mdpi.com/2071-1050/10/12/4607/pdf>.
- Keaulana, S., J. J. Chung-Do, I. Ho-Lastimoso, P. W. Hwang, K. Ho, T. Radovich, M. Spencer, L. Albinio, I. Rogerson, L. Keli‘iholokai, and K. Deitschman. 2019. Waimānalo pono research hui: Establishing protocols and rules of engagement to promote community-driven and

- culturally-grounded research with a native Hawaiian community. *The British Journal of Social Work* 49(4): 1023–1040. <https://doi.org/10.1093/bjsw/bcz012>.
- Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, and T. Thierer. 2012. Geneious basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28(12): 1647–1649. <https://doi.org/10.1093/bioinformatics/bts199>.
- Kelly, M. 1983. Na mala o Kona: Gardens of Kona. Bernice P. Bishop Museum Department of Anthropology Report 83-2. Honolulu: Bernice P. Bishop Museum.
- Kirch, P. V., J. Holson, and A. Baer. 2009. Intensive dryland agriculture in Kaupō, Maui, Hawaiian Islands. *Asian Perspectives* 48(2): 265–290. <https://doi.org/10.1353/asi.2009.0006>.
- Ladefoged, T. N., M. W. Graves, and J. H. Coil. 2005. The introduction of sweet potato in Polynesia: Early remains in Hawai'i. *Journal of the Polynesian Society* 114(4): 359–374.
- Lee, D. W. and J. H. Richards. 1991. Heteroblastic development in vines. In: *The biology of vines*, eds. F. E. Putz and H. A. Mooney, 205–243. Cambridge, United Kingdom: Cambridge University Press.
- Loveless, M. D. and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics* 15(1): 65–95. <https://doi.org/10.1146/annurev.es.15.110184.000433>.
- Muñoz-Rodríguez, P., T. Carruthers, J. R. I. Wood, B. R. M. Williams, K. Weitemier, B. Kronmiller, D. Ellis, N. L. Anglin, L. Longway, S. A. Harris, M. D. Rausher, S. Kelly, A. Liston, and R. W. Scotland. 2018. Reconciling conflicting phylogenies in the origin of sweet potato and dispersal to Polynesia. *Current Biology* 28(8): 1246–1256.e12. <https://doi.org/10.1016/j.cub.2018.03.020>.
- Nagata, K. M. 1985. Early plant introductions in Hawai'i. *Hawaiian Journal of History* 19: 35–61.
- Napihelua, M. L. 1857, March 4. Uala! Uala! Ka Hae Hawaii [Hawaii] 2(1): 1.
- Oberholtzer, L., C. Dimitri, and C. Greene. 2005. Price premiums hold on as U.S. organic produce market expands. Washington, D.C.: United States Department of Agriculture, Economic Research Service, VGS-308-01, 1–22. <https://naldc.nal.usda.gov/download/41261/PDF>.
- Platt, A., M. Horton, Y. S. Huang, Y. Li, A. E. Anastasio, N. W. Mulyati, J. Ågren, O. Bossdorf, D. Byers, K. Donohue, and M. Dunning. 2010. The scale of population structure in *Arabidopsis thaliana*. *PLoS Genetics* 6(2): e1000843. <https://doi.org/10.1371/journal.pgen.1000843>.
- Poole, C. F. 1952. Seedling improvement in sweet potato. Technical Bulletin No. 17. University of Hawaii Agricultural Experiment Station, Honolulu, Hawaii.
- . 1955a. Sweet potato genetic studies. Technical Bulletin No. 27. Hawaii Agricultural Experiment Station, College of Tropical Agriculture, Honolulu, Hawaii. <http://hdl.handle.net/10125/40997>.
- . 1955b. The sweet potato in Hawaii. Circular 45. Hawaii Agricultural Experiment Station, College of Tropical Agriculture, University of Hawaii. <http://hdl.handle.net/10125/53712>.
- . 1959. Improvement in yield of sweet potato clones. *Proceedings of the American Society for Horticultural Science* 73: 445–452.
- Pukui, M. K. 1983. 'Ōlelo No'eau: Hawaiian proverbs and poetical sayings. Honolulu: Bishop Museum Press.
- Randell, R. A. and C. W. Morden. 1999. Hawaiian plant DNA library II: Endemic, indigenous, and introduced species. *Pacific Science* 53: 401–417. <http://hdl.handle.net/10125/712>.
- Rooke, T. C. B. 1855. Report on the sweet potato (*Convolvulus batata*). In: *Transactions of the Royal Hawaiian Agricultural Society* 38–43.
- Roselius, K., W. Stephan, and T. Städler. 2005. The relationship of nucleotide polymorphism, recombination rate and selection in wild tomato species. *Genetics* 171(2): 753–763. <https://doi.org/10.1534/2Fgenetics.105.043877>.
- Rosero, A., L. Granda, J.-L. Pérez, D. Rosero, W. Burgos-Paz, R. Martínez, J. Morelo, I. Pastrana, E. Burbano, and A. Morales. 2019. Morphometric and colourimetric tools to dissect morphological diversity: An application in sweet potato [*Ipomoea batatas* (L.) Lam.]. *Genetic Resources and Crop Evolution* 66: 1257–1278. <https://doi.org/10.1007/s10722-019-00781-x>.
- Roullier, C., G. Rossel, D. Tay, D. Mckey, and V. Lebot. 2011. Combining chloroplast and nuclear microsatellites to investigate origin and dispersal of New World sweet potato landraces. *Molecular Ecology* 20(19): 3963–3977.

- <https://doi.org/10.1111/j.1365-294X.2011.05229.x>.
- Roullier, L. Benoit, D. B. McKey, and V. Lebot. 2013. Historical collections reveal patterns of diffusion of sweet potato in Oceania obscured by modern plant movements and recombination. *Proceedings of the National Academy of Sciences* 110(6): 2205–2210. <https://doi.org/10.1073/pnas.1211049110>.
- Scaglione, R. 2005. Kumara in the Ecuadorian Gulf of Guayaquil? In: *The sweet potato in Oceania: A reappraisal*, 35–42. Sydney: University of Sydney.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9(7): 671–675. <https://doi.org/10.1038/nmeth.2089>.
- St. Onge, K. R., T. Källman, T. Slotte, M. Lascoux, and A. E. Palme. 2011. Contrasting demographic history and population structure in *Capsella rubella* and *Capsella grandiflora*, two closely related species with different mating systems. *Molecular Ecology* 20(16): 3306–3320. <https://doi.org/10.1111/j.1365-294X.2011.05189.x>.
- Taitano, N., V. Bernau, L. Jardón-Barbolla, B. Leckie, M. Mazourek, K. Mercer, L. McHale, A. Michel, D. Baumler, M. Kantar, and E. van der Knaap. 2018. Genome-wide genotyping of a novel Mexican Chile Pepper collection illuminates the history of landrace differentiation after *Capsicum annuum* L. domestication. *Evolutionary Applications* 12(1): 78–92. <https://doi.org/10.1111/eva.12651>.
- Takahashi, M. 1937. Self and cross fertility and sterility studies of the sweet potato (*Ipomoea Batatas* [L.] Poir). Master's thesis, University of Hawai'i at Mānoa, Honolulu, Hawaii.
- Tavaré, S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. *Lectures on Mathematics in the Life Sciences* 17: 57–86.
- Vitousek, P. M., T. N. Ladefoged, P. V. Kirch, A. S. Hartshorn, M. W. Graves, S. C. Hotchkiss, S. Tuljapurkar, and O. A. Chadwick. 2004. Soils, agriculture, and society in precontact Hawai'i. *Science* 304(5677):1665–1669. <https://doi.org/10.1126/science.1099619>.
- Wang, X. P., X. Cheng, and Z. Yun-Jiao. 2019. The complete chloroplast genome of a wild sweet potato, *Ipomoea trifida* (Kunth) G. Don. *Mitochondrial DNA Part B* 4(1): 2063–2064. <https://doi.org/10.1080/23802359.2019.1574672>.
- Yan, L., X. Lai, X. Li, C. Wei, X. Tan, and Y. Zhang. 2015. Analyses of the complete genome and gene expression of chloroplast of sweet potato [*Ipomoea batata*]. *PLoS ONE* 10(4): e0124083. <https://doi.org/10.1371/journal.pone.0124083>.
- Yang, J., M. H. Moeinzadeh, H. Kuhl, J. Helmuth, P. Xiao, S. Haas, G. Liu, J. Zheng, Z. Sun, W. Fan, G. Deng, H. Wang, F. Hu, S. Zhao, A. R. Fernie, S. Boerno, B. Timmermann, P. Zhang, and M. Vingron. 2017. Haplotype-resolved sweet potato genome traces back its hexaploidization history. *Nature Plants* 3: 696–703. <https://doi.org/10.1038/s41477-017-0002-z>.
- Yen, D. E. 1963. The New Zealand Kumara or sweet potato. *Economic Botany* 17: 31–45. <https://doi.org/10.1007/BF02985351>.
- . 1974. *The sweet potato and Oceania: An essay in ethnobotany*. Honolulu: Bishop Museum Press.
- Zheng, X., D. Levine, J. Shen, S. M. Gogarten, C. Laurie, and B. S. Weir. 2012. A high-performance computing toolset for relatedness and principal component analysis of SNP data. *Bioinformatics* 28(24): 3326–3328. <https://doi.org/10.1093/bioinformatics/bts606>.