Diversity and Value of Extant Hawaiian Sugarcane (*Saccharum officinarum* [L.]) Cultivars

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Sugarcane is one of the most economically important crops with particular cultural and economic significance in the Hawaiian Islands. The historical influence of sugarcane in Hawai‘i tends to overshadow the fact that Native Hawaiians cultivated dozens of unique varieties of sugarcane for almost a millennium before the arrival of Europeans. The objective of this study was to characterize the genetic and phenotypic diversity of sugarcane to reexamine the relationships between traditional Hawaiian sugarcane varieties and heirloom cultivars from elsewhere in the Pacific. To this end, a morphological assessment utilizing 95 phenotypic characteristics of 53 extant cultivars held in ethnobotanical collections was conducted, along with genetic assignment using 6,570 polymorphic SNP markers on 156 diverse varieties. In investigating distinct traditional cultivars of extant sugarcane collections in Hawai ‘i as “Hawaiian,” our findings demonstrated the need for intimate knowledge and relationships with accessions in order to make meaningful interpretations of genetic and phenotypic data. Based on over 15 years of involvement with the heirloom Hawaiian canes and the traditional and contemporary uses, we demonstrated and discussed the unique value of these cultivars, and their potential to contribute to economics, sustainability, and the preservation of cultural heritage.

Keywords: Sugarcane, Saccharum, Hawaiian, Heirloom, Kō, Morphology, Genetics, SNP

Introduction

Sugarcane, known as kō in the Hawaiian language, is the single most important crop in the colonial history of Hawai‘i (Gray 1972; MacLennan 1997 2014; Wilcox 1997). The overwhelming impact of the sugarcane plantations in Hawai‘i overshadows the reality that Native Hawaiians introduced sugarcane to the Islands nearly a millennium before Europeans arrived; that Hawaiians

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cultivated sugarcane extensively in a broad range of ecosystems using diverse agricultural systems; that dozens of native varieties of kō were developed; and that sugarcane played a vital role in the culture and livelihood of Native Hawaiians, as it did for many other indigenous peoples across the Pacific (Abbott and Shimazu 1985; Brigham 1899, 1906; Handy 1940; Kamakea 1872; Whistler 2009).

Traditional Management

Hawaiian *mahi ʻai* (cultivators) were among the most adept farmers in the Pacific, sustaining agriculture for centuries across an impressive range of soils and climates (Lincoln and Vitousek 2017). Even a basic understanding of the indigenous planting and horticulture gives reason to respect the extensive knowledge developed and encoded into traditional practices. One of the many areas in which Hawaiian agriculturalists excelled was the systematic differentiation, identification, and naming of their crop varieties (Handy 1940). These varieties were, and are still, utilized in ways that enhance the resilience, production, and practicality of agriculture (Lincoln et al. 2017; Lincoln and Vitousek 2016, 2017; Marshall et al. 2017). Hawaiian cultivators devised and applied new ways of planting that differed from those found elsewhere in Polynesia, driven in part by the vastly different environments of Hawaiʻi. As Hawaiʻi has one of the densest concentration of diverse habitats and ecosystems on the planet (Asner et al. 2005), it follows that Hawaiian cultivators had perhaps the densest diversity of agroecological forms and practices (Lincoln et al. 2018).

Historic Loss of Cultivar Diversity

Indigenous Hawaiian horticulturalists distinguished upwards of 80 sugarcane cultivars according to their appearance, usage, and environmental tolerance (Lincoln 2020). The initial development of sugarcane plantations in Hawaiʻi, beginning in 1835, utilized native kō cultivars. Although the Hawaiian cultivars were developed and selected for use in diversified cropping systems, many still exhibited superior production in plantation settings compared to available cultivars at that time, and local cultivars were exported to plantations around the world (Artschwager and Brandes 1958; Moir and Caum 1928). Starting in 1854 with the heirloom Tahitian cultivar "Otaheiti," an influx of introduced varieties displaced Hawaiian kō in the plantations and even in many backyards and other small–scale plantings (Lincoln 2020; Vitrac 2017). Popular introduced varieties were given Hawaiian names and adopted into cultural norms (for instance, "Otaheiti" became known as "Lahaina" and was a popular backyard variety). In the early 1900s, a world–renowned breeding program at the Hawaiian Sugar Planters' Association (HSPA) began, which produced tens of thousands of new hybrid varieties that replaced heirloom varieties in the plantations, but not elsewhere. In the late 1800s, as a precursor to the establishment of its breeding program, HSPA conducted a statewide reconnaissance of kō, collecting several hundred accessions along with minimal local ethnographic information, often only a name. With a certain irony, the sugarcane industry simultaneously preserved the physical germplasm while eroding the cultural knowledge regarding it (Table 1). In the early 2000s, significant efforts began to restore the knowledge systems of Hawaiian kō (Kagawa–Viviani et al. 2018), and it was quickly realized that multiple shortcomings in the germplasms existed. For example, the names attached to the modern collection were often incorrect. There was poor documentation or differentiation between native Hawaiian, introduced heirloom, and early hybrid varieties. There was no identification process for verifying or identifying a cultivar.

Reviving Cultivar Identity and Associated Knowledge

A renewed interest in kō is seen in two distinct, but related, movements. The first is part of a larger movement to reclaim Native Hawaiian identity, knowledge, and culture (Low 2013), including a substantial return to traditional crops and cultivation (Kagawa–Viviani et al. 2018). The second is largely a result of the renewed interest in food diversity, culture, and sustainability—the so–called foodie movement (Sloan 2013). In the past decade, several local distillers

Table 1. Brief timeline of sugarcane in Hawai'i

Date	Event
~1000	Sugarcane introduced to Hawai'i by Polynesians, cultivated widely in diverse agroecosystems
1778	Arrival of Europeans to Hawai'i
~1800	First sugarcanes varieties exported from Hawai'i
1835	Establishment of first sugar plantation in Hawai'i
1854	Introduction of first non-Hawaiian heirloom sugarcane varieties to Hawai'i
1895	Hawaiian Sugar Planters' Association established with breeding program ensuing
1974	Initial decline of sugarcane industry
1970–1990	Establishment of Hawaiian ethnobotanical sugarcane collections at multiple botanical gardens
2005–2015	Establishment of local distilleries using Hawaiian sugarcane
2016	Closure of last sugar plantation in Hawai'i

of rhum agricole—rum produced directly from pressed sugarcane juice as opposed to byproducts such as molasses—have emerged. These companies tend to rely on heirloom varieties, at least in part, because of the marketing potential of these traditional varieties. This renewed interest in kō has paralleled an increase of plantings at several different scales, and we can confidently say that more heirloom cane is being grown in Hawai'i now than at any time in the past century.

Genotyping and phenotyping are common tools to aid in providing clarity to germplasm collections. Hawaiian cultivators had many cultural–specific morphological descriptions of sugarcane (Kagawa–Viviani et al. 2018). Contemporary breeding programs have used a broad range of morphological traits to discern their collections (Artschwager and Brandes 1958). In the past decades, molecular markers have been used widely to genotype and classify the relationships among various accessions in sugarcane, such as amplified fragment length polymorphism (AFLP) (Besse et al. 1998; Hoarau et al. 2001) and simple sequence repeat (SSR) (Pan et al. 2007; Silva et al. 2012). Recently, utilization of abundant, cost–efficient, and high throughput genotyping markers, specifically single–nucleotide polymorphisms (SNPs), is becoming increasingly important in crop cultivar identity discerns (Aitken et al. 2014; Seeb et al. 2011). The development of an Axiom Sugarcane100K SNP array based on two SNP datasets (Song et al. 2016; You et al. 2019) was used to genotype a panel of 469 sugarcane clones with multiple ploidy levels, and was approved as a reliable and efficient genotyping performance.

The revival of knowledge and interest of the canes have further resulted in their increased usage and study. This has necessarily increased the number and type of stakeholders, and the number of interactions between stakeholders. Social interactions around native crops in Hawai'i and elsewhere have resulted in constructive collaborations and highly antagonistic conflicts. Figure 1 explores the pathway to collection rejuvenation and ways to create sustainable use of the resorted resources, as we aim to elicit in this paper. While the primary data of this paper focus on the processes of Fig. 1A, we pull upon our experience and informal market assessments to consider the broader implications of this research in the social interactions of rejuvenated usage of traditional cultivars and the interactions between stakeholders as illustrated in Fig. 1B.

Objectives

The primary objectives of this study were to apply morphological and genetic documentation to sort through ambiguities in the ethnobotanical collection of Hawaiian canes, and to situate Hawaiian cane diversity within the broader diversity of the Pacific noble canes. Detailed morphology was conducted on 53 heirloom canes held in extant collections, and SNP genetic analysis was conducted on 156 varieties

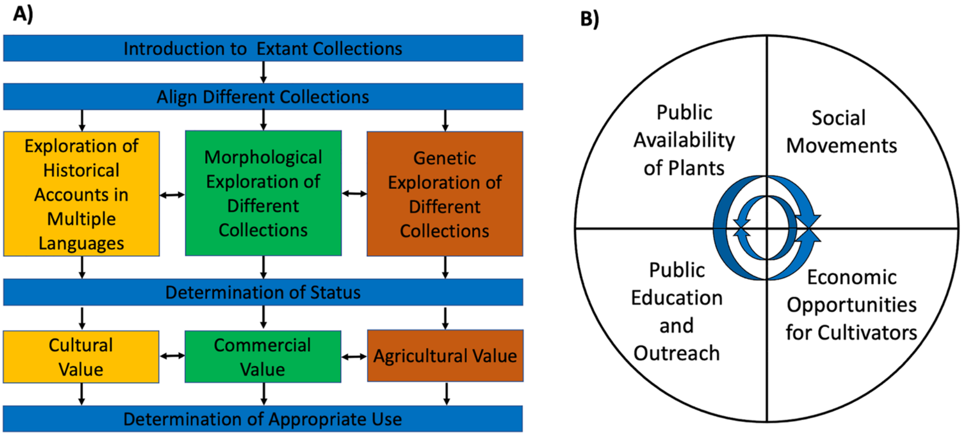


Fig. 1. **A** Reinvigorating historic collections, **B** Creating a virtuous cycle of restoration

representing a broader suite of canes, with 46 canes included in both the morphological and genetic assessments. We further discussed the multiple values of the canes to the various stakeholders and their role in preserving and enhancing that value to further situate the study within the socio–cultural context of the heirloom sugarcane stakeholders today.

Materials and Methods

We use the term “traditional” in this text as a synonym for “heirloom” and “heritage,” regardless of the origin. We reserve the term “Hawaiian” or “traditional Hawaiian” for cultivars that we assume were developed and named by indigenous Hawaiian farmers from germplasm present in the islands prior to 1778. The terms “variety” and “cultivar” are used interchangeably.

Morphological Characterization

In situ conservation of the cane specimens were observed at 11 different sites on four islands in Hawai‘i, including six ethnobotanical gardens, two research collections, and three private collections. Included in the morphological study were 53 individual cultivars each represented by at least four sites, totaling 384 plantings (Electronic Supplementary Material—ESM Appendix 1). For each accession, 95 morphological parameters (ESM Appendix 2) were recorded that included both qualitative (color, shape, etc.) and quantitative (length, girth, etc.) descriptions of plant traits. Plant traits were selected to represent both indigenous (Lincoln 2020) and western (Artschwager and Brandes 1958) observations, with an emphasis on easily observable traits that could be applied by farmers and other non–botanists. At each site, independent observations were made by three observers, with one observer in common for all sites. Data was amalgamated across observers and sites to the best representative values and converted to nominal, ordinal, and continuous numerical data for analysis as appropriate. Multiple Factor Analysis (MFA) and K–means clustering was conducted by using the FactorMiner package (Lê et al. 2008) in R (R. C. Team 2013). Prior to MFA, an assessment of the variables was conducted by (1) normalizing the data to z–scores by dividing the difference of each element of a variable and the variable mean by the standard deviation, (2) conducting a two–sample t–test for all variables using all combinations of well–confirmed provenance classes (defined as Hawaiian, Pacific Heirloom, and Hybrid), and (3) removing all variables that did not produce significant results (defined as $P < 0.05$ and t–value $>|2|$). The remaining (36) parameters were used to execute MFA. Variables with rotated factor loading of less than 0.3 or with cross loading greater than 0.3 were further removed. The remaining (19) parameters were used for clustering analyses.

Genetic Characterization

A total of 156 sugarcane accessions housed at the Hawai'i Agricultural Research Center's (formerly the Hawaiian Sugar Planters' Association) germplasm collection in Maunawili, O'ahu, were included for the genetic characterization (ESM Appendix 3). The 156 accessions were represented in three different subsets: (1) 46 canes that were morphologically characterized, (2) 78 canes representing the core ethnobotanical collection that includes Hawaiian and presumed Hawaiian canes, early Pacific heirloom introductions, and early generation hybrids, and (3) 156 canes that includes a broader set of Pacific heirloom varieties. A newly emerging leaf was collected from each accession, surface cleaned and sterilized with 70% alcohol, and stored at –80ºC until DNA extraction. DNA was extracted using the DNeasy Plant Kit (Qiagen, Valencia, CA) and subsequent genotyping was conducted with a previously developed Sugarcane SNP array (You et al. 2019). Although sugarcane is a polyploid crop (octoploid), only the single dose SNP markers were selected and used for the sugarcane SNP array (You et al. 2019). Therefore, the SNP genotypes at each site on array are called as: 0, 1, 2, and –1; respectively, homozygous, single dose heterozygous, double dose heterozygous, and missing. SNPs that could not be detected due to low assay quality are treated as "n/a" for purposes of downstream data analysis. Genetic assignment was determined using (PCA) conducted in SNPRelate (Zheng and Zheng 2013). A bayesian phylogeny was constructed using MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001) and applying a GTR substitution model with the following specifications: gamma rate variation with four categories, Markov Chain Monte Carlo (MCMC) using 4 heated chains (1,000,000 in length) with a subsampling frequency of 500, and burn–in length of 10,000.

Results

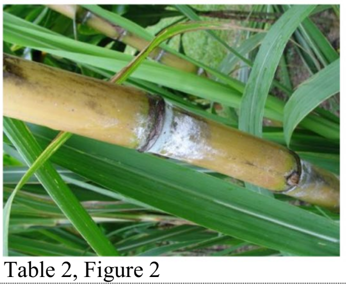
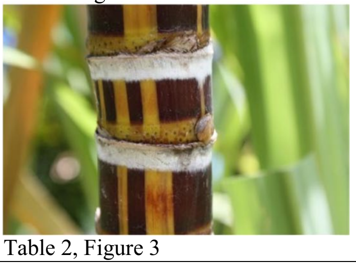
Ethnographic research illuminated the status of many of the heirloom canes in the Hawaiian ethnobotanical collections (Lincoln 2020). In cases where varietal names and morphological descriptions were consistent across early nineteenth century Native Hawaiian testimony, historical documentation, and contemporary collections, the variety could be firmly ascribed as being a Hawaiian cultivar. However, in many cases the origin and status of the canes remained ambiguous, necessitating a new analysis of morphological and genetic data. To illustrate this study and the historical thread, we utilize several varieties as case studies and introduce them more thoroughly here in Table 2, as modified from Lincoln 2020.

Morphological Characterization

Documentation of morphology was done using established, although in some cases simplified, traits (Artschwager and Brandes 1958; Lincoln 2020). Most phenotypic traits were consistent across environments; however, aspects of color, growth form, and to a lesser extent pubescence varied. While in most cases trait variation was reasonably narrow, for some traits, particularly stalk color, the variation could be substantial. Using repeated observations from different sites, the "standard" expression of phenology was selected. In some cases, determination of the appropriate metric was important. For instance, while measurements of leaf length and leaf width varied considerably across environments, the ratio of the leaf length to the leaf width showed little variation and was quite useful.

Phenological analysis demonstrated diverse morphologies that typically could reasonably be distinguished. However, there were multiple instances where different accessions demonstrated identical morphology, or differed very subtly in size and vigor. For some morphologically identical individuals, the canes were suspected to be the same variety, particularly for canes without ethnobotanical information attached. For instance, three canes thought to be of Hawaiian origin were donated to collections from Maui, and were held under the simple names "Maui Cane X." These suspected Hawaiian cultivars were morphologically identical to known Hawaiian cultivars and was considered good confirmation of their identity. Of the eight instances of identical phenotypes, we believe that six cases are truly synonymous, including our highlighted canes of "Honaunau #2" and "Not Kokea."

Table 2. "Case study" canes used to illustrate results from morphological and genetic assignments

Cultivar Name(s)	Description
Pakaweli  Table 2, Figure 1	"Pakaweli" is an archetype Hawaiian variety that is consistently recorded throughout Native testimony, historical documentation, and contemporary records. It exhibits all of the most common morphological traits of the Hawaiian varieties and is easily identifiable by its occasional bright pink leaf variegation.
Honaunau #2 Not Kokea  Table 2, Figure 2	These two separate accessions are both unknown, but suspected, Hawaiian varieties. "Honaunau #2" was collected in the late 1800s without any associated ethnographic information. "Not Kokea" was held in collections for several decades as "Kea"—the most famous and referenced cane in Hawaiian ethnobotany—but was renamed in the 1990s based on personal testimony from HSPA.
Manulele Tolo Mauga  Table 2, Figure 3	Manulele is the name of a famous Hawaiian variety that is well documented in ethnohistorical testimony, but "Manulele" held in collections today does not match the historical descriptions. Lincoln (2020) suggested that todays 'Manulele' appears similar to another Pacific heirloom, 'Tolo Mauga.'

MFA and clustering results were highly dependent on which traits were selected. The use of all 95 morphological features did not result in the best separation of varieties known to be of Hawaiian, Pacific, or breeding origin, likely due to correlation between variables. Using only 19 parameters (Fig. 2; ESM Appendix 2), reasonable separation of Hawaiian, Pacific, and hybrid varieties was possible. At eight clusters: (1) the three known hybrids and two suspected hybrids form a distinct cluster; (2) the largest cluster (n = 18) consisted exclusively of varieties that are confidently Hawaiian cultivars, including our archetype "Pakaweli"; (3) the three smallest clusters included known and presumed Hawaiian varieties; and (4) the last three clusters consisted of a mix of Pacific heirlooms and varieties of questionable provenance (Fig. 2).

Genetic Similarity

Of the 100,097 SNP markers on the array, 6,570 sites were polymorphic and thus were used to genotype the 156 individuals (ESM Appendix 3; ESM Appendix 4). Three different subsets were considered in order to best consider the relative relatedness of groups of canes, and to connect the genetic results to the ethnobotany of the individuals: (1) 46 canes that were morphologically characterized, (2) 78 canes representing the core ethnobotanical collection that includes Hawaiian and presumed Hawaiian

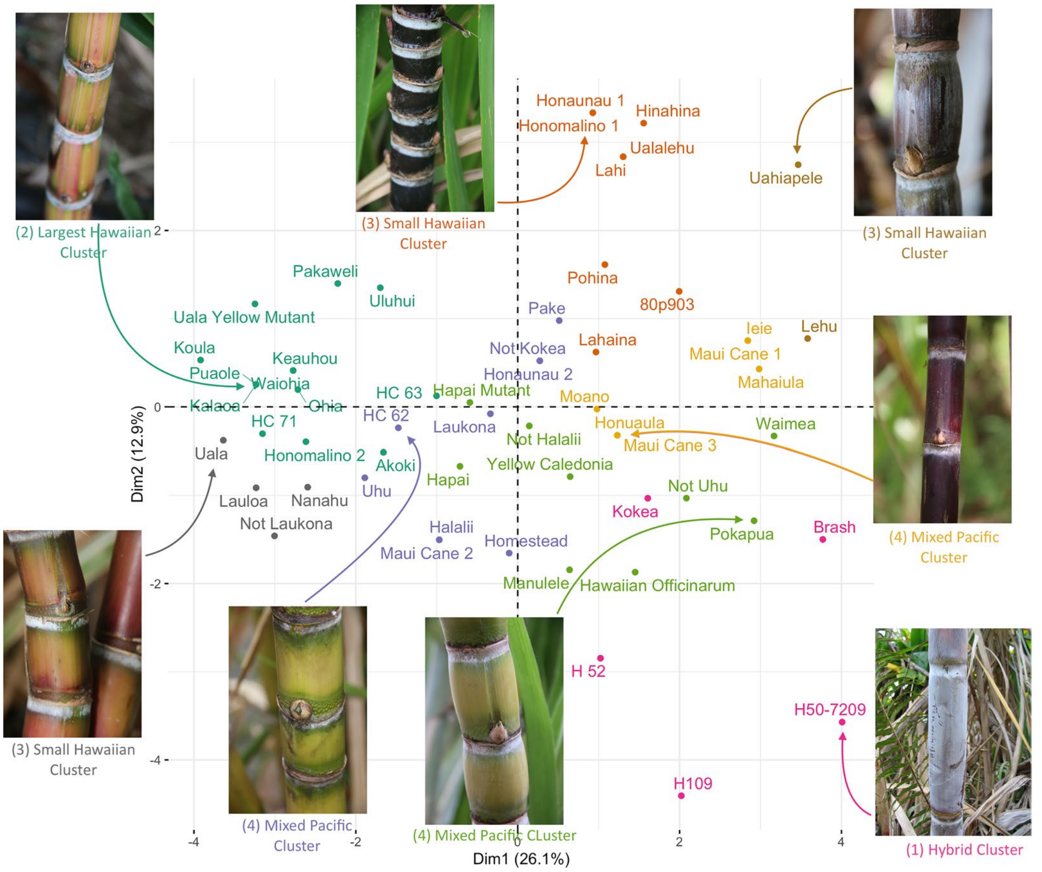


Fig. 2. Multiple Factor Analysis according to 19 morphological features that generated best separation of known cane classifications, colored by k–means clustering (n = 8) and displaying a representative cultivar from each cluster

canes, early Pacific heirloom introductions, and early generation hybrids, and (3) 156 canes that includes a broader set of Pacific heirloom varieties.

Examining only the 46 varieties included in the morphological analysis, the cluster analysis revealed a strong clustering of the presumed Hawaiian varieties, with only "Pohina" as a potential outlier (Fig. 2a). At this scale we also saw some "inliers" of unknown varieties, suggesting that they may be of Hawaiian origin. "Pakaweli" as our archetype Hawaiian variety is situated within the largest genetic cluster. Zooming out to include all cultivars comprising the core ethnobotanical collection, there are several strong clusters of Hawaiian cultivars that often include varieties of unknown (but suspected Hawaiian) origins (Fig. 2b). "Pakaweli" is again in the largest clusters of Hawaiian canes. "Honaunau #2" and "Not Kokea" appear genetically identical and situated within a strong Hawaiian genetic cluster, while "Manulele" appears in an ambiguous cluster composed of known Pacific heirlooms and heirlooms of questionable provenance. In the full complement of canes, the Hawaiian clusters are still apparent, although with overlap and integration of Western and Eastern Pacific accessions (Fig. 2c). Hybrid accessions and different species did not cluster with one another or with cultivars from any particular geography. Cultivars and their mutant sports—somatic mutations that commonly arise—clustered very close to one another in genetic space. A small sub–study was embedded by sampling a number of individuals representing "Manulele" and its mutant phenotypes, which can all be seen to cluster very closely.

Discussion

Historic collections of Hawaiian plants have often been well maintained with few misidentifications (e.g., Winnicki et al. 2021). However, in the case of sugarcane, the large, early influx of Pacific heirloom germplasm and the subsequent breeding programs created more convoluted relationships than within other Hawaiian crop collections (Kagawa–Viviani et al. 2018). Previous research highlighted some discrepancies and ambiguities (Lincoln 2020). Here, we observe reasonable agreement between morphological and genetic methods to distinguish heirloom sugarcane cultivars from accessions derived from other geographic regions, but argue that neither genetics nor morphology alone is yet adequate to identify heirloom cultivars in collections, and that both are only interpretable with strong historical understanding.

Assessment of Hawaiian Canes

There have been two major pieces of work previously focused on the relationships of Hawaiian sugarcanes, with one morphologic (Moir 1932) and one genetic (Schenck et al. 2004) study. In order to compare our results to previous studies, we overlaid our genetic data with the (1) seven clusters defined by Schenck et al. (2004) using 228 genetic markers, and (2) two major groups of canes (split into 11 "families") defined by Moir (1932) using a mix of morphological features and observed mutations (Fig. 3).

Moir (1932) defines his two morphologic families based on overall growth stature, breaking the canes up in short/stocky/erect ("Badila type") and lankier/recumbent ("Lahaina type"). These two families are seen to be well distributed in the genetic cladogram (Fig. 4B), as might be expected for any single morphological trait. While the sample size is small, there does appear to be clustering families within the broader matrix. Some of the individual families that Moir (1932) suggests are supported, but for the most part they are not clustered together.

Genetically, results reasonably align with Schenck et al. (2004) (Fig. 4A). Identical clusters were seen (e.g., 5, 6) and the unclustered individuals in the previous study were generally separated from other canes in this study. The two largest and most closely related clusters from Schenck et al. (2004)—the large core clusters of Hawaiian canes (i.e., clusters 1 and 2)—occupied overlapping space and showed different clustering patterns in our current study.

Using a combination of ethnographic, common garden, and genetic information, we built upon previous work of historical relationships, genetics, and observations (Artschwager and Brandes 1958; Kamakea 1872; Lincoln 2020; Moir 1932; Moir and Caum 1928; Schenck et al. 2004) to discuss the authenticity and diversity of the cultivars. Strong genetic and morphologic clustering suggests that the core Hawaiian ethnobotanical collection is authentically Native Hawaiian. The very close genetic relationship of the core Hawaiian cluster may indicate that these varieties arose through somatic mutation rather than seed. Some of the Native Hawaiian varieties are known to be able to mutate into each other and back, likely defined by large phenotypic changes (e.g., variegation or other color changes) resulting from single gene mutations. This is seen in the almost indistinguishable clustering of 14 individuals consisting of "Manulele" and its mutants (Fig. 2c). Within the "Manulele" block, varieties are only weakly differentiated genetically, suggesting few other mutations occurring in concert with the known observable successive somatic mutations. This is similar to Hawaiian kalo (*Colocasia esculenta*), where families of related varieties are known to mutate into each other (Winter 2012).

A few cultivars thought to be Native Hawaiian appear to be more closely related to canes that originated in other geographies, such as "Pohina." While it may be tempting to read into the genetic separation as indicating that such outliers are not authentically Hawaiian, strong ethnobotanical evidence suggests that these are indeed Hawaiian. This may result from cultivars from different geographies being introduced and used by Native Hawaiians over the course of time, such as through long–distance trade. Alternatively, ancient breeding may have produced more genetically diverse individuals.

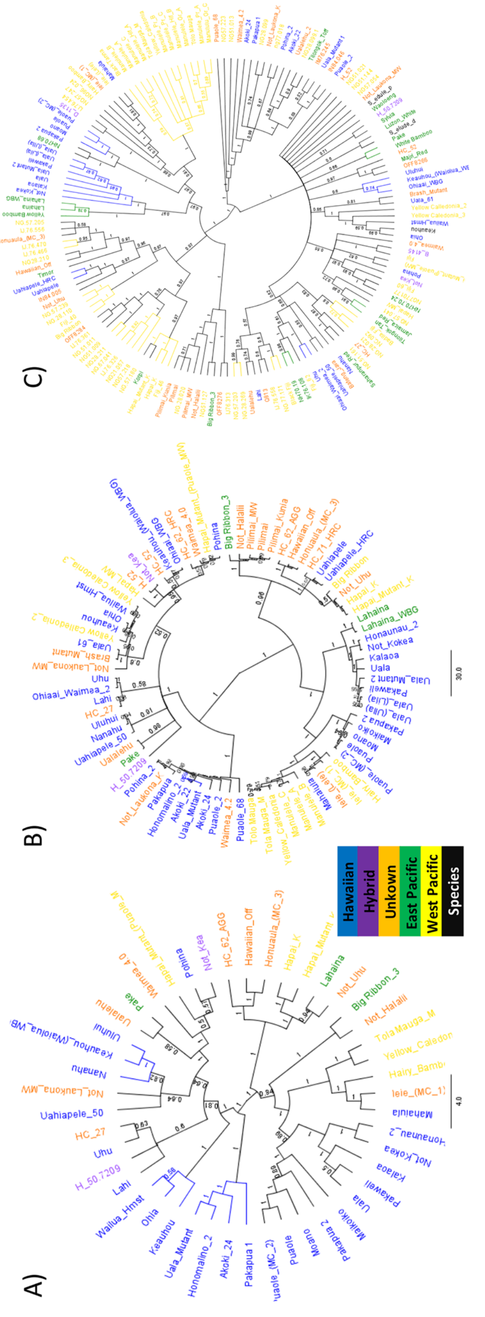


Fig. 3. Bayesian phylogeny of Pacific sugarcane from 6,570 SNP markers for **(A)** morphologically characterized 53 Hawaiian sugarcanes, **(B)** the core ethnobotanical collection of 78 Hawaiian sugarcanes, and **(C)** all 156 Hawaiian, Pacific, and hybrid canes used in this study

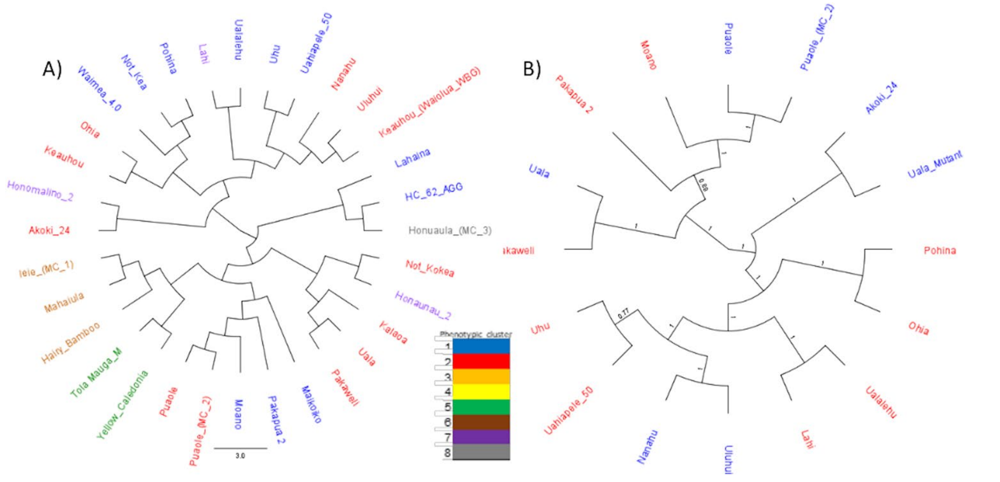


Fig. 4. Comparison to historical studies by (**A**) Canes in this study that were also present in Schenck et al. (2004) and (**B**) Canes in this study that were also present in Moir (1932)

Schenck et al. (2004) suggests that there were seven closely related clusters of Hawaiian sugarcanes, with two of those clusters (the "Manulele" and "Mahaiula" clusters) now believed to be non–Hawaiian clusters. Although the number of clusters changes depending on where cutoffs are defined, we suggest that in general five to seven clusters of Hawaiian canes are evident in the cladograms, supporting the previous findings. The separate groups may relate to individual introduction or breeding events (Mangelsdorf 1956). Like Schenck et al. (2004), we also observed that there is substantial genetic variation outside of core clusters of Hawaiian varieties. This may represent a broad diversity within Hawaiian canes, or could be manifestations of errors in the collections. Unfortunately, even using multiple tools and sources of evidence resulting from 15 years of study, for some varietal names we still cannot definitively say if it is a Hawaiian variety or not.

In some cases, individuals of unknown or questionable provenance were confirmed as introduced canes, such as "Manulele." Conversely, this study provides initial evidence that some canes of unknown provenance, such as an unknown variety collected in the Wailua Hawaiian Homestead, may be a Hawaiian cultivar. Although the genetics and morphological situation can suggest authenticity, neither technique can indicate with certainty the provenance of the cane and further work to connect unknown canes to historical descriptions is needed.

The analysis suggests that there are several accessions that have acquired new names. This could be due to similarity with lost accessions or adoption of introduced genotypes. Of particular interest, and confusion, is regarding the name "Kokea"—the most famous and referenced of all Hawaiian varieties. Our analyses support previous findings (Schenck et al. 2004) that the cultivar currently held in collections as "Kokea" is actually a commercial hybrid variety. A separate accession previously held as "Kokea" was renamed "Not Kokea" when an HSPA verifier indicated that the cane was mislabeled in the early 1990s. Lincoln's (2020) study suggested that "Honaunau #2" was an excellent potential match to the historical descriptions of "Kokea," and in this study "Honaunau #2" and "Not Kokea" were shown to be morphologically and genetically identical, and situated strongly in the Hawaiian clusters for both analyses. Collectively, the results support suspicions that the true "Kokea"—thought to have been lost—may have been found.

In their extensive documentation of noble canes, Artschwager and Brandes (1958) state that "of the groups of noble canes the Hawaiians are most homogeneous (pg. 81)." This may be expected in that Hawai'i represents one of the extremities of Polynesian settlement, and the diversity of crops was narrowed through the wayfinding process of settlement (each new island settled only received a subset of the diversity from the departing island). The grouping of Hawaiian cultivars in both morphology and genetic space together suggests that Polynesian farmers had clear phenotypic characteristics that were preferable for local cultivation and that they preferred to use these as parents in breeding. However, the individual accessions that are grouped with other geographies suggests that if a useful trait was identified then it was readily adopted and then used in cultivation. This could explain both the narrow morphology and broad genetic diversity spread within the context of the broader Pacific collection.

Value of Historic Threads

The value of this work was in the integration of multiple lines of evidence. In addition to the genetic and morphological data, the study benefited from extensive ethnographic and historical research (Lincoln 2020) as well as intimate and prolonged relationships with the individual varieties. We feel that deep knowledge of the historical thread was integral to any interpretation of data regarding the canes. Even high–quality studies are inadequate for appropriate interpretation without a strong understanding of the varieties over time. For instance, Schenck et al. (2004) starts from the assumption that "Manulele" is a Hawaiian cultivar, and concludes that.

> "Moir (1932) cited an ancient Hawaiian legend concerning Manulele ("flying bird") and considered it to be a native, as did Kamakea (1872). However, our results support Wilfong (1883), who listed it as a later import."

The reality of this situation is that multiple cultivars exist under the name "Manulele." The "Manulele" accession does not match the historical descriptions by Moir (1932) and Kamakea (1872), suggesting that there was a Native Hawaiian "Manulele" (now possibly lost) and an introduced "Manulele" (shown in this study to be identical with the Pacific heirloom "Tolo Mauga"). Thus, relying on accession names to represent an individual variety without extensive documentation and regular verification is an inadequate approach to maintaining living collections. Indeed, we argue that *relationships* to the varieties are needed to understand who they are, where they come from, and about their characters and performances over time and across space.

There is a revived interest in indigenous crops and cropping systems, in Hawai‘i and globally (Chang et al. 2019; Kagawa–Viviani et al. 2018; Lincoln et al. 2018). In light of growing environmental and social issues associated with conventional agriculture and food systems, many people are acknowledging holistic benefits from traditional, diversified farming and food (Altieri 2004, 2018). These crops and cultivation systems represent multiple forms of value. A growing number of studies demonstrate traits in indigenous and heirloom crops that have been lost in modern systems. Further, indigenous cultivars may preserve other valuable characteristics, such as physiological traits, chemical compounds, or flavor profiles. An example that received wide popular attention was the mucilage–based nitrogen–fixing maize variety from Oaxaca, Mexico (Van Deynze et al. 2018). While receiving less attention, sugarcane has been shown to be a substantial contributor to nitrogen inputs through both symbiotic and asymbiotic nitrogen fixation pathways (Lincoln and Vitousek 2016; Reis et al. 2007). Similarly, a study of the rhizosphere in maize varieties that have undergone modern breeding shows a decline in microbial associations that contribute to increased N losses (Favela et al. 2021). Indigenous crop selection is not immune from these patterns (e.g., Xing et al. 2012); however, indigenous crops represent less breeding and selection pressure, and selection for low–input farming systems. Heirloom varieties—such as kō—and their traits will be needed in developing diversified, low–input agricultural systems since the necessary traits have been inadvertently bred out of modern hybrids (Garnett et al. 2013).

Biocultural relationships bring multiple forms of cultural value to indigenous crops. Restoration of indigenous crops and cropping systems in Hawai‘i has been shown to strongly engage individuals in embracing traditional values and worldview, which can manifest in outcomes related to education, personal values, self–identify, historical perception, and so on (Chang et al. 2019; Kagawa–Viviani et al. 2018;

Langston and Lincoln 2018). Use of traditional varieties helps to connect to specific histories and practices that allow the unfettered transmission of traditional knowledge, embedded into *mo'olelo* (stories) told regarding the individual cultivars (Kagawa–Viviani et al. 2018).

In Hawai'i, a growing industry of boutique distilleries focus on rum agricole: rums distilled from sugarcane juice as opposed to molasses, and typically only distilled to their final alcohol concentration instead of to 70-80% and diluted as with most rums. The "pure" process of distilling preserves the unique taste and terroir in the final product. These agricole distillers rely extensively on heirloom canes due to their higher sugar content and richer flavor profiles, despite the increased difficulty in growing them. A brief survey of two local liquor stores shows that all locally distilled products have an average price (and standard error) of about USD 48/L (4.7), while the average price of locally distilled rhum agricole is USD 152/L (20.3). While some of this value is generated from the heirloom traits of the canes and the distilling process, some of the value is certainly derived from the marketing of Hawaiian culture and history. The history of Hawaiian sugarcanes, including specific stories and ethnohistories, are used extensively to enhance the identity and marketability of the brands.

Unfortunately, different forms of value that can be derived from Hawaiian sugarcane can become contentious. The economic and biocultural values of the crop mean that there are diverse stakeholders in heirloom varieties who may have different priorities regarding their interactions with and representations of the varieties. Often, economic and biocultural values are considered in conflict with each other—one seen as extractive of the other. In particular, the commodification of Hawaiian knowledge and stories is typically seen as a form of appropriation, with increasing activism by Native Hawaiians and allies to prevent disingenuous representation and marketing of Hawaiian culture (Hall 2005). In essence, stories of the Hawaiian canes are valuable marketing whether or not they are accurate. Industry producers, whose target audience are primarily tourists and export markets, do not have to answer to the community or the public institutions that have worked to preserve and restore the varieties and their knowledge. This can create tension in which the industry partners are able to benefit from the ethnobotany but are not beholden to it. However, examples from Hawai'i show that different stakeholder values can be synergistic (e.g., Bremer et al. 2018; Langston and Lincoln 2018). The growing agricole industry has provided new opportunities for preservation, dissemination, and observations of the Hawaiian canes, as well as new platforms for sharing of indigenous perspectives. However, there are also instances of amplifying errors and misrepresentation that could be improved upon, particularly when ambiguities exist in the collections.

Increased availability of both the canes and the knowledge regarding the canes that have resulted from this and other studies have, in part, powered the social movements and the economic opportunities involving the Hawaiian cane varieties. In return, the social and economic movements have provided opportunities for further increase in the cultivars and the opportunities to understand them. For instance, the germplasm collections often only maintain a single planting of each variety, making the observations of the sporadic mutation infeasible. However, under commercial production there are hundreds of culms of a single variety grown, providing the opportunity to observe multiple mutations of the varieties, such as what enabled the "Manulele" mutation sub–study embedded in our data. Because the understanding of the varieties is in a state of flux, it is important to communicate well among stakeholders to ensure that the canes are properly represented. Sometimes this is not as simple as informing a distillery that a name has changed or a status has been updated; rather, it involves building a relationship between a distillery and those who value the canes culturally, allowing the importance of appropriate representation to be conveyed directly.

We suggest that it is essential that different stakeholder groups communicate, acknowledge their strengths and weaknesses in preserving historical threads, and collaborate where possible. The role of large institutions—HSPA in the case of Hawai'i—is that they are important contributors to cultivar maintenance, but the amount of material preserved by institutions is traded off against errors arising more frequently and reduced ability to intimately know the individuals. Community institutions, such as the

Hawaiian ethnobotanical gardens, are essential in building communities of enthusiasts and making the varieties more broadly available, leading to increased usage and interest. The development of commercial industries provides new opportunities for research and documentation, and new avenues to tell the stories of the Native Hawaiian canes. However, these pathways can only be leveraged through engagement, and creating strong networks for the sharing of information, collaboration of research, and ensuring appropriate representation of the canes is essential. Such networks rely on relationships that require constant maintenance in order for all stakeholders to achieve all of the goals to achieve sustainable use of the canes.

Conclusion

Through the exploration of an economically and culturally important crop we have shown the importance of many different types of analysis (ethnographic, historical, morphological, genetic) that can be combined to create a fuller understanding of the plants we interact with every day. While the emergence of powerful genetic analyses are important tools, they cannot clearly answer the relationship and provenance of traditional cultivars without a broader contextual understanding of the individual varieties. By exploring the many angles, which are sometimes contradictory, it is possible to come to an understanding not only of the relationships of plants to one another but also of the relationships between people and plants.

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