NAVIGATING THE ERA OF NEO-HEIRLOOM TOMATOES (*SOLANUM LYCOPERSICUM* L.): DEVELOPING AN HEIRLOOM MARKET TYPE CLASSIFIER USING HIGH-THROUGHPUT PHENOMICS AND MACHINE LEARNING

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAIʻI AT MĀNOA IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE
IN
TROPICAL PLANT AND SOIL SCIENCES

July 2022

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Acknowledgments

To the people in my life who have afforded me the patience, wisdom, and perspective to see beyond self-doubt, I am forever grateful.

Abstract

Although there are various informal definitions for heirloom tomatoes (*Solanum lycopersicum* L.), there is no official botanical classification or certification scheme. Novel hybrid cultivars advertised as 'heirloom-like' exemplify the term's application as a phenotypic descriptor, departing from the term's established conceptions. Two field trials were conducted in Hawai'i to screen cultivars representing traditional heirlooms, heirloom hybrids, and commercial cultivars to explore this concept. We observed significant differences in total and marketable yields (kg/plant) within and between three tomato market classes. Phenotypic traits related to fruit morphology, color, and physicochemical quality were used to develop a Multilayer Perceptron Neural Network (MLPNN) classifier to investigate whether the heirloom archetype could be defined. The model could distinguish between traditional heirlooms, heirloom hybrids, and commercial cultivars with an accuracy rate of 85%. Global and local agnostic tests identified traits for physicochemical quality, color, distal end shape, blockiness, and the latitudinal section as most influential for distinguishing the heirloom class. This study demonstrated that a wide range of phenotypic traits could be selected to target the heirloom ideotype; however, quality standards should be considered to preserve the integrity and value of the heirloom insignia.

Keywords: *Heirloom Tomato, Solanum lycopersicum L., Fruit Quality, Phenomics, Classification, Machine Learning, Ideotypes*

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Chapter 1. Historical and Contemporary Perspectives on the Heirloom Tomato

Introduction

Tomatoes (*Solanum lycopersicum* L.) are ubiquitous in diets across cultural and geographic regions, with around 85% of the world's nations contributing to producing ~1.8 MT (million tonnes) globally in 2020 (FAOSTAT, 2022). Despite their widespread utility, fresh market tomatoes have come under increasing scrutiny for their poor sensory attributes (Estabrook, 2018; Jabr, 2012; Oltman et al., 2014; Everts, 2012; Wang & Seymour, 2017). Modern tomato quality is a recurring topic in the public domain, where scathing reviews and comparisons to "cardboard" and "wet-paper-towels" have become familiar rhetoric (Everts, 2012; F Jabr, 2012; Milius, 2012; Mirsky, 2013). The shortcoming of modern tomato cultivars has prompted a growing body of researchers to investigate the molecular and genetic mechanisms contributing to these criticisms and their implications for future improvement (Alseekh et al., 2021; Folta & Klee, 2016; Gao et al., 2019; Klee & Tieman, 2018; Tieman et al., 2012, 2017; Zhao et al., 2019; Zhu et al., 2018). Public and academic narratives on modern tomatoes vary in tone and objective, but each sector has unanimously adopted heirlooms to illustrate the preferred tomato archetype (Jordan, 2007; Panthee et al., 2013; Panthee & Gardner, 2014; Vargas et al., 2015).

Heirloom tomatoes have attracted public attention since appearing in popular culture during the 1980s (Jordan, 2007). In the past four decades, the term heirloom has evolved from an icon of the local-food movement to a designation for tomatoes with distinctive features that command premium prices. While demand for traditional heirloom tomatoes remains high, their supply is generally limited to direct sales within regional food systems. Many of these varieties' production traits and shelf life do not meet modern commercial standards (Healy et al., 2017). Consumers in the twenty-first century have been characterized by their increased interest in food systems and preference for diverse, high-quality produce (Ekelund & Jönsson, 2011). To meet these demands, industry professionals are shifting away from prioritizing traits of interest to production and distribution stakeholders and toward a consumer-directed model for selecting desirable fruit phenotypes (Folta & Klee, 2016). Many prominent seed distributors are offering a new fresh market category, broadly described as ‘heirloom-like' (Table 1.1). Advertisements for these new hybrid cultivars pander to heirloom enthusiasts with taglines like "old-world goodness with a twist of modern world traits" (Vitalis Organic Seed, 2021) while also appealing to growers with high yields, disease resistance, and durable fruits. Using the term heirloom is not regulated by an authoritative body or recognized as an official botanical classification. The conventions and proprietary rules (UPOV, 1991) that govern the naming of new varieties are definitive, but the characterization of terminologies such as heirloom, heritage, landrace, folk, or farmer varieties remains subjective. Public confusion and debate have surfaced with the emergence of these new hybrid tomatoes that are vibrantly colored, unusually shaped, and advertised for their seemingly 'heirloom-like' features.

Therefore, the objectives for this review are two-fold: i) present a historical narrative for the fresh market tomato in the United States to account for the heirloom’s origins, and ii) contextualize heirloom tomatoes in a modern breeding and production framework. The scope of this review focuses primarily on the United States market, but many concepts can be applied to traditional cultivars in other geographic regions. The overarching goal of this study is to identify areas where further research is needed and to generate additional perspectives for ongoing discussions on what constitutes an ‘heirloom.’

Domestication and Diversification

As with heirloom nomenclature, tomato taxonomy has been a source of contention for centuries. Advancements in molecular technology affirmed one side of this debate, validating the species grouping in *Solanum* and restoring Linnaeus's original classification of *Solanum lycopersicum* L. (Spooner et al., 1993; Knapp, 2002; Peralta & Spooner, 2007). Providing consistent and universally accepted terminology establishes a baseline for communicating in the sciences. Unfortunately, public confusion over the species' taxonomic status will likely persist, as the former description (*Lycopersicon esculentum* Mill.) remains in texts from the last two decades. Tomato and its wild relatives are native to the Andean region of South America (Peralta et al., 2008; van Andel et al., 2022). Blanca et al. (2012; 2015; 2022) described the currently accepted domestication model as a ‘two-step’ process originating with the small-fruited wild species *S. pimpinellifolium* L. Evidence suggests *S. pimpinellifolium* L. naturally evolved during a northern migration to form the semi-domesticated species *S. lycopersicum* var. *cerasiforme* (Dunal) D.M. Spooner, G.J. Anderson & R.K. Jansen (Peralta & Spooner, 2007; Blanca et al., 2015; 2022). Upon its arrival in Mesoamerica, the cherry-sized fruit of *S. cerasiforme* was formally domesticated in Mexico, giving rise to the cultivated species *S. lycopersicum* L. (Bai & Lindhout, 2007; Razifard et al., 2020; Blanca et al., 2022). The Spanish conquest of Mexico in 1521 marked the beginning of the tomato's rise to global prominence, following which it joined several crops transported to Europe at this time (Bergougnoux, 2014; Caramante et al., 2021). Although detailed historical accounts for the species’ domestication in Mexico are lacking, botanical records for the earliest tomatoes to arrive in Europe indicate it was already in an advanced domesticated state (Daunay et al., 2007; Peralta et al., 2008). In their recent paper, Andel et al. (2022) presented an overview of the phenotypes reported in prior and newly identified records from 1544 to 1555. While these samples constitute the only genetic material spread throughout Europe, by the eighteenth century, farmer selections had created regional populations with a wide variety of fruit characteristics (Foolad, 2007; Rick & Fobes, 1975; Tanksley & McCouch, 1997; Casañas et al., 2017). The different fruit morphologies linked with this era were described as ribbed, oblong, deeply grooved, round, and flattened, with hues ranging from red to orange, yellow, pink, and brown (van Andel et al., 2022). Today, these features reflect the dominant aesthetic for the heirloom market. However, it would require millennia for novel fruit traits to be universally valued over uniformity (Goldman, 2008; Smith, 1994).

Before they were ‘Heirlooms’

After arriving in Europe, accounts of the tomato’s utility varied from ornamental to medicinal and, for those brave enough, culinary (Peralta & Spooner, 2007; Hyman, 2019). Superstitions over the fruit’s toxicity delayed its culinary use in Europe and later in the United States, as rumors persisted within European colonies (Estabrook, 2018; Rick, 1978; Foolad, 2007). As tomatoes spread across the future United States in the late eighteenth century, consumption began normalizing in pocketed regions. This gradual integration into society and culture can be seen by the fruit's first depiction in American artwork in 1795, where Raphaelle Peale’s *Still-life with Vegetables and Fruit* depicts a singular red fruit, whose shape can only be described as lobed to a degree of deformity (Smith, 1994; Hyman, 2019). If advertised today, this tomato would likely be assigned to the 'specialty' class and command a premium over ‘standard’ slicing varieties that dominate the modern fresh market. This notion would likely shock seedsmen from the mid-nineteenth century, as they were eager to present the American public with its first large, round, and perfectly uniform tomato.

According to folklore, misconceptions about the tomato's toxicity were dispelled after a gentleman ate the fruit in front of spectators at a Salem, New Jersey courthouse. Although various adaptations of this legend remain in perpetuity, a 1908 bulletin released by West Virginia University's agricultural research station credited the 1848 canning operation at Lafayette College (Easton, Pennsylvania) for fostering the nation's new favorite crop (Munson, 1908). Initial market availability was limited to cherry, plum, and pear-shaped fruits that varied in hues of red and yellow (Male, 1999). Seeds for larger fruits circulated within communities, but they were not commercialized because their irregular shapes were considered unmarketable. It was still common practice in the 18th century to engage in informal breeding by saving seeds from productive crops and detecting novel phenotypes arising from random mutations or outcrossing. Although public interest in breeding was piqued following Darwin’s release of On the Origin of Species (1837), laws of inheritance and Mendelian genetics were foreign concepts, even to seedsmen. Even though plant breeding had yet to become a scientific discipline, there was an influx of supposedly new tomato varieties hitting the market. A prevalent concern during this timeframe was that many of the new cultivars in seed catalogs would 'run out,' a phrase used to convey issues of segregating populations released as distinct varieties. This phenomenon was reflected in the varietal descriptions in The Field and Garden Vegetables of America by Fearing Burr (1865). The author prefaces his description of twenty common varieties with the caveat “…some are merely nominal, many are variable or quite obscure, and a few appear to be distinct, and, in a degree, permanent.” The regularity with which growers purchased unreliable seeds engendered public mistrust of tomato's burgeoning seed industry, forcing some growers to declare, “My chief reliance is to raise seeds and plants of my own that I know to be good” (Horace, 1870). In the brief course of tomato's history in the United States, concurrent narratives have emerged at the threshold of modernization. Despite being separated by more than a century, growers' attitudes in the eighteenth century are reminiscent of grassroots movements in the 1970s. In response to consumer complaints, industries frequently respond with novel innovations. Today, this is reflected by the unified quest to improve fruit quality by incorporating "heirloom-like" features. However, around the turn of the nineteenth century, the most significant reforms to the seed industry were attributed to the work of one Ohio seedsman.

Becoming an Industry

Alexander Livingston is widely regarded as America's first tomato breeder (Boswell, 1937; Estabrook, 2018; Hyman, 2019; Liedl et al., 2013; Munson, 1908; Peralta & Spooner, 2007; Smith, 1994; Stevens & Rick, 1986; Watson, 1996). The impact his varieties had on the country's tomato industry earned him this distinction, but it was the ethos he imparted on the market that maintained his legacy. Like many of his contemporaries, the Ohio seedsman was eager to present America with what he considered the 'ideal' tomato: large, round, smooth, and uniform in all respects. Upon the 1870 release of his first variety, *Paragon*, Livingston declared it "...the first perfectly and uniformly smooth tomato ever introduced to the American public" (Livingston, 1893). The validity of his assertion is arguable, but his sentiments allude to achieving a distinct variety with fixed traits. What has inevitably become Livingston's lasting contribution was conceptualizing trait selection based on the needs of different markets. Framed within a period where the scale and geographic range of commerce were rapidly expanding, Livingston identified the demand for a tomato that could compete in an industrial market space. By prioritizing traits such as firmness, uniform ripening, and shelf life, Livingston was ahead of his time. However, rather than approaching his trade through scientific theory, Livingston operated under misguided breeding principles. Detailed in his book, *Livingston and the Tomato,* the seedsman dismissed hybridization as “violat[ing] the laws of nature” and proposed novel traits should only be obtained through chance differentiation observed in select stock (Boswell, 1937). According to his own admissions, Livingston could not explain this phenomenon beyond attributing it to some higher power. However, he quickly relayed to his customers that the common people could not replicate the caliber of his breeding. In responding to some of his most frequent inquiries: “Can farmers and market gardeners grow their own seed and save this expense?” he answered a resounding no. Livingston’s memoir reflects an emerging narrative that allocated cultivar development to an industry rather than the farmer. America’s first tomato breeder illustrates a dichotomy of the tomato's place in American culture. While his successes paved the way for the rise of the private seed sector in the twentieth century, his legacy is inherently linked to the role heirlooms play in the current market. Livingston envisioned breeding tomatoes to correspond with individual market sectors, each distinguished by the producer and consumer demands. This ethos is reflected in the evolution of the processing, fresh, and now, ‘specialty’ markets. Today, Livingston’s collection meets many of the prescribed criteria to be considered heirlooms. In an ironic twist of fate, the man whose life work was to create 'perfectly uniform' fruit now has his seed categorized by a term synonymous with the features he sought to eliminate.

Expansion of the Tomato Industry During the Twentieth Century

"During the war... home gardeners could not do much experimenting. We had to stick with the tried and true. But now that the war is over...our dreams 'turn toward new varieties."
-1946 USDA radio announcement foreshadowing changes in the tomato industry

Before the 1940s, informal crop improvement and seed-saving were still prevalent among farmers, gardeners, and hobby breeders. The cultivars developed in this manner are widely referred to as landraces (a term not mutually exclusive with heirloom) and are distinguished by their adaptations to local growing conditions and expression of regional quality preferences (Zeven, A.C., 1998; Casañas et al., 2017). The USDA's 1937 Yearbook acknowledged these early breeding efforts but regarded landraces as inferior to modern varieties that were more durable and productive across different environments. Historically, the boundary between privately and publicly bred cultivars was not as distinct as it is today, with many commercial cultivars originating from public institutions, farmers, and amateur breeders. When the first F_1-hybrid *Single-Cross* was introduced in 1946, this balance of power fundamentally changed. The innovation and technology that followed World War II marked a discernible shift in food production and distribution. With the onset of synthetic fertilizers and improved mechanization, there was a preference for cultivars that could withstand post-harvest handling during long-distance distribution (Sangam & Ortiz, 2019). According to Hoenig (2018), these factors led to a second industrialization phase in the tomato industry, during which the agricultural sector became increasingly centralized and homogenized. Although backyard gardeners and small-scale farms continued to grow traditional varieties, grocery supply chains sought favor in the lower prices and uniformity of F_1-hybrids.

The Heirloom

"The American public is not satisfied with old things, however good they may be."
- A.W. Livingston

Even with his foresight into the requirements for the twentieth-century market, Alexander Livingston could not have predicted that consumers would inevitably seek tomatoes from the past. There has emerged a discourse around heirloom tomatoes that is as diverse as the varieties that bear the insignia. Despite its frequent inclusion in academic and public texts, the term heirloom has maintained an ambiguous status (Table 1.2). Botanical classifications afford clarity and consistency in scientific communications, but this precedent is disrupted when colloquial terms like heirloom become universally relevant. Further confusion arises from several terms (Table 1.1) that are used interchangeably with heirloom, each of which has become a topic of discussion in its own right (Berg, 2009; Casañas et al., 2017; Saxena & Singh, 2006; Villa et al., 2005; A. C. Zeven, 1998). Although heirloom discourse is conspicuously devoid of concrete definitions, engaging with the nuance of its interpretation can be just as insightful.

In the literature, perspectives on the heirloom tomato are governed by two initiatives: preserving biodiversity and improving quality. The most comprehensive historical accounts of the heirloom tomato in popular culture have come from the social sciences (Jordan, 2007, 2015; Joseph et al., 2017). In many instances, these analyses follow a recent trend in which commercial tomatoes are used to personify industrial agriculture and investigate the boundaries of commercialization for consumers (Estabrook, 2018; J. Hoenig, 2018; Hyman, 2019). Although separated by fifty years, many of these contemporary works mirror similar arguments conveyed by the original grassroots movements that catalyzed old tomato varieties back into the fresh market. Kingsbury (2009) and Ekelund et al. (2011) attribute these movements to a transition into 'late modernity,' a cultural epoch defined by romanticizing relics of the past as a response to rapid technological change. By the mid-20th century, advances in agrochemicals, mechanization, and modern plant breeding had dramatically altered the scale and efficiency of food production (J. M. Hoenig, 2018). As agricultural systems evolved, plant breeding consolidated in the private sector, where research and development focused primarily on F1-hybrids for commercial operations (Dwivedi et al., 2019). While these innovations contributed to historic gains in crop productivity, rural farmers and home gardeners grew concerned as F1-hybrids quickly displaced open-pollinated cultivars in seed catalogs (Jordan, 2015; Pollan, 1994). Kent Whealy, founder of the non-profit Seed Savers Exchange, became a vocal critic of the commercial seed industry in recurring newspaper articles and trade journals (Curry, 2019; Jabs, 1984; Lacy, 1996; Mother Earth News, 1982). Whealy was among many home gardeners and small-holders who argued that the rise of F1-hybrids in the seed trade threatened the loss of valuable germplasm (Navazio, 2012; Pardey et al., 2013; Wattnem, 2016; Wincott, 2018). Although Kent Whealy is often credited with popularizing heirlooms in the 1980s, Jordan (2015) contends that the heirloom tomato has developed two distinct identities over time. The plight of organizations like the Seed Savers Exchange exemplifies the first era of the heirloom tomato, personified by conservation and biodiversity campaigns. As the local food movement gained momentum, the heirloom tomato became a poster child for regional cuisine in upscale restaurants and culinary reviews (Ibsen & Nielson, 1999; Jabs, 1984; Pesci & Brinkley, 2021; Pollan, 1994; Schneider, 1996). Due to the rising media attention and association with artisanal cuisine, the term 'heirloom' shifted from its origins in conservation and local food to a secondary identity founded in consumer marketing and the social elite (Jordan, 2015; Joseph et al., 2017).

Heirlooms in a Modern World: Lost in Translation or Interpretation?

As consumers look for alternatives to the standard fresh market tomato, the price and demand for heirloom cultivars have steadily climbed over the past 30 years (Ozores-Hampton et al., 2012; Stark, 2008). Recent studies attribute this to a legacy of breeding decisions that favored production-end stakeholders at the expense of the quality features pertinent to consumers (Bauchet et al., 2017; Causse et al., 2010; Healy et al., 2015; Wang & Seymour, 2017; Zhao et al., 2019). Where consumers value sensory attributes and novelty, historical breeding objectives for fresh market tomatoes have focused on yield, disease resistance, uniformity, and extended shelf life (Baldwin et al., 2000; Folta & Klee, 2016; Tieman et al., 2017). Folta & Klee (2016) examine the nuances underlying these issues, arguing that while breeding in the last 50 years contributes to existing consumer complaints, the industrialized nature of the modern food system contributes significantly to the poor sensory attributes people report. Recent molecular and genetic studies have shed light on complex polygenic traits like flavor (Baldwin et al., 2000; Bauchet et al., 2017; Pereira et al., 2021; Tieman et al., 2017; Zhao et al., 2019), prompting broader discussions on the impact of historical breeding practices on genetic diversity. While improving fruit flavor remains a goal for many breeding programs, researchers are also pursuing morphology and color to satisfy consumers' demand for ‘heirloom-like’ quality (Alonso et al., 2011; Panthee & Gardner, 2014; Rodríguez-Burruezo et al., 2005).

Extensive work has been carried out to characterize the phenotypic diversity found in vintage (i.e., heirloom) germplasm (Bhattarai et al., 2016; J. Blanca et al., 2021; Cortés-Olmos et al., 2015; Ercolano et al., 2008; Panthee, Labate, & Robertson, 2013). Studies of this nature generally describe germplasm at the individual level, but in some cases, European landraces have been described at the population level (Caramante et al., 2021; Fortes et al., 2016). Although the phenotypic diversity in traditional germplasm has been extensively documented, accounts of their genetic diversity have varied (Labate, 2021; Mohan et al., 2016; Pereira et al., 2021; Vargas et al., 2015). Several authors have addressed the necessity for scholarly consensus about the classification of germplasm that falls under terminology such as heirloom, landrace, farmer, traditional, and folk varieties (Berg, 2009; Casañas et al., 2017; Saxena & Singh, 2006; Villa et al., 2005; A. C. C. Zeven, 1998). Despite these attempts, the characterization of these terms tends to vary by region and context (Table 1.1). Two prevailing schools of thought dominate the literature: the European model, which emphasizes preservation and treats landraces as cultural objects (Berg, 2009; Casañas et al., 2017; Rocchi et al., 2016; Saxena & Singh, 2006; A. C. Zeven, 2002), and the United States model, which focuses on identifying suitable germplasm to satisfy consumer demand (Causse et al., 2003; Panthee et al., 2012; Panthee et al., 2013; Tieman et al., 2017; Tombesi et al., 2020; Xu et al., 2013). These models resonate with the heirloom tomato's historical narratives, where Europe (notably Spain and Italy) embodies grassroots conservation movements, and the United States reflects the era of artisanal markets and the bourgeoisie. Despite these differing perspectives, seed companies in Europe and the United States are developing 'Neo-heirloom' tomatoes in response to decades of quality concerns. These cultivars are F1-hybrids that generally exhibit the fruit phenotypes that have become characteristic of traditional heirlooms. Even though this novel market type routinely promotes its 'heirloom-like' quality, there is not enough research to support these claims. Although 'Neo-heirlooms' constitute a step toward incorporating consumer interests into breeding programs, more investigation into the production and phenotypic quality of these genotypes is necessary if the 'Neo-heirloom' is to succeed in penetrating the market (Table 1.2).

Reconciling the Consumer and Producer Voice in Breeding Priorities

Heirloom tomatoes have been adopted as the poster child for opposing interests, first as the icon for the slow-food movement, now as the industry's caricature of consumer preference. Although phenotypically diverse, because heirloom varieties are homozygous, inbred lines, they possess limited genetic variability. Breeders and producers will need to balance their objectives for incorporating the phenotypes that consumers demand and broadening the cultivated tomato genome. The needs of the producer and consumer are not mutually exclusive. To meet the challenges of a changing climate, stakeholder interest at both ends of the market need to cohabitate the breeding process (Campanelli et al., 2015; Ceccarelli et al., 2009; G. K. Healy et al., 2017; Shelton & Tracy, 2016). While significant progress has been made, many outstanding questions require further investigation:

1. Does the demand for heirlooms correspond with outward fruit characteristics and purportedly superior flavor, or is it attributable to their link with movements that reject the agro-industrial food system?
2. If ‘Neo-heirlooms’ are mass-produced, do they merit the same market price as traditional varieties?
3. If a tomato could incorporate the features desired by both producer and consumer, would the phenotype satisfy the heirloom archetype?

In the last 50 years, the concept of ‘heirloom’ has evolved continuously under the influence of geographical location, social ideologies, and consumer perception. The subjective nature of prior classifications necessitates that this class is objectively defined to facilitate market research and provide additional perspectives on the history and future trajectory of heirloom tomatoes.

Chapter 1. Tables

Table 1.1. Examples of informal definitions and descriptions of heirloom, landrace, and related terms as they appear in the literature.

Source	Terminology/Description
LeHouillier & Male (1995) **Male (1999)**	<u>*Heirloom*</u> **Family**: Selected and stabilized by farmers or home gardeners and maintained within a family or region. **Commercial**: Varieties introduced to the public by seed companies before 1940. **Created**: Varieties deliberately created by crossing two known heirlooms, or an heirloom and a hybrid, and then stabilized. **Mystery**: Result from natural, unintentional, cross-pollination, or spontaneous mutation, and then stabilized by a grower. This category is distinguished by including varieties generated in modern times.
Watson (1996)	<u>*Heirloom*</u> **1)** Must be open-pollinated and true-to-type. Not inclusive of recent commercial F_1-hybrid that are stabilized. **2)** Developed more than 50 years ago and maintained by either family, ethnic, religious, or tribal groups. Recognizes that more stringent definitions exclude seed from any commercial companies. **3)** Must have a history of origin, either verifiable or based on oral tradition.
Blanca et al. (2022)	<u>*Traditional*</u> Varieties developed by traditional farmers through intuitive breeding and cultivated prior to systematic breeding programs. *Cites vintage, landraces, and heirlooms to be synonymous with traditional.
Williams & St. Clair (1993) **Sims et al. (2011)**	<u>*Vintage*</u> Cultivars released during or before the 1960s and/or were developed before the application of Mendelian principles.
Zeven (1998)	<u>*Autochthonous Landrace*</u> A variety with a high capacity to tolerate biotic and abiotic stress, resulting in high yield stability and an intermediate yield level under a low input agricultural system.
Saxena & Singh (2006)	<u>*Farmer/Folk*</u> Varieties developed by farmers/communities that are homogeneous and stable for specific traits.
Casañas et al. (2017)	<u>*Landrace: a proposed concept for the future*</u> Cultivated varieties that have evolved, and may continue to evolve, within a defined ecogeographical area under the influence of the local community. Permits adapting landraces to new production systems, through unconscious or conscious selection by farmers and breeders, and/or incorporating modern breeding technology.

Table 1.2. A list of seed companies and distributors that currently offer ‘heirloom-like’ tomato varieties. Where provided, the seed collections' names and the distributors' marketing descriptions are included.

Seed Company **-** *Collection name*	**Seed Distributor**	**Marketing Description**	**Website**
Gautier Semences	Johnny’s Selected Seeds	*French Heritage Collection*	https://www.johnnyseeds.com
Vitalis Organic Seeds - *Mixologist Collection*	Osborne Quality Seeds	*Hybrid Heirloom*	https://www.osborneseed.com
Ball-PanAmerican Seed Co. - *Heirloom Marriage™*	Burpee	*Heirloom Marriage™*	https://www.panamseed.com
TomaTech-Nirit Seeds Ltd. - *Specialty – The Musketeers*	n.a.	*Specialty* *‘The Muskateers’*	https://www.tomatech.com
Yüksel Tohum - *Village-types*	Paramount Seeds	*Heirloom-type*	https://paramountseeds.com
Harris Morgan-HM Clause - *Exotics*	Seedway	*Specialty*	https://www.seedway.com
Santa Sweets - *UglyRipe®*	n.a.	*UglyRipe®* *‘Heirloom Tomato’*	http://www.santasweets.com

Chapter 2. Developing an Heirloom Market Type Classifier Using High-throughput Phenomics and Machine Learning

Introduction

The tomato industry has historically operated within two distinct market domains: fresh and processing (USDA, 1983, 1991). This distinction has facilitated targeted research tailored to the specific needs of each supply chain; however, this dynamic has been disrupted over the past thirty years as changing consumer preferences have caused a divergence in the fresh market (J. Blanca et al., 2015). Although improving flavor and fruit quality has recently received increased attention (Gao et al., 2019; Saliba-Colombani et al., 2001; Tieman et al., 2017; Zhao et al., 2019), public complaint over the matter has been continuously voiced since the 1970s (Hightower, 1972; Klee & Tieman, 2018). Since the early 1990s, consumers have come to associate the term 'heirloom' with colorful, atypically shaped, and flavorful tomatoes (Dwivedi et al., 2019). Due to the stark contrast between these characteristics and the typical commercial prototype, heirloom tomatoes have evolved into a ‘specialty’ subclass within the fresh market (Grassbaugh et al., 1999; Johnston, 2011; Joseph et al., 2017).

While some heirloom enthusiasts attribute their preference to novel organoleptic properties, others claim their preference stems from nostalgia for preindustrial agriculture. (Jordan, 2007). In the years following World War II, technological innovations that increased the scale of production and distribution profoundly altered the agricultural industry. With the advent of agronomic chemicals and improved mechanization, commercial breeders focused on developing cultivars that could endure post-harvest handling throughout the supply chain (Klee & Tieman, 2018; Worthington et al., 1978). Although backyard gardeners and small-scale farms continued to grow more delicate varieties, grocery supply chains sought favor in the lower prices and uniformity of hybrid slicers. The tomato market remained homogenous until it was disrupted again in the early 1980s, instigated by celebrity chefs and food critics showcasing the heirloom tomato as their new culinary muse (Hugh et al. 2017). Coinciding with the birth of the local food movement, the heirloom tomato became the poster child for regional cuisine as consumers sought more diversity in their produce options. Rather than being a fleeting trend, demand for heirloom tomatoes has increased over time, as evidenced by its proportional impact on market prices. Today, varieties such as Cherokee Purple and German Johnson are household names and can be purchased at artisanal markets for roughly twice the price of standard fresh market varieties (USDA: Specialty Crops, 2020). Recent trends in trait selection among tomato breeders demonstrate that industry professionals are cognizant of consumers' shifting preference for tomatoes with novel shape and color attributes. In lieu of maintaining the classic red beefsteak archetype, new hybrid cultivars are promoted as having 'heirloom-like’ fruit quality with modern production traits. Although heirloom tomatoes have acquired numerous colloquial definitions, such as being at least 50 years old, open-pollinated, or specific to a region with a traceable ancestry, there is no official botanical classification or accreditation system in place (Harland and Craxton, 2009). In the absence of established standards and regulations, the 'heirloom-like' insignia has evolved into a phenotypic descriptor rather than a designation of heritage or pedigree.

While the sociocultural debate on what genuinely qualifies as an heirloom tomato may continue for years, it is possible to quantitatively examine the properties that distinguish this unique class. With the advent of high-throughput phenotyping tools, such as the Tomato Analyzer (TA v. 4.0) software (Gonzalo et al., 2009), the precision and efficiency of collecting objective measurements for fruit morphology and color have significantly improved (Granier & Vile, 2014). Numerous studies have used TA measurements and fruit physicochemical properties to characterize quality features in traditional germplasm (Figàs et al., 2015; Nankar et al., 2020; Panthee, Labate, McGrath, et al., 2013). However, no existing research has used these parameters to broadly classify the ‘heirloom’ archetype. Machine learning (ML) and statistical data mining have become popular tools in the plant sciences for processing and identifying valuable insights from phenomics data (Gill et al., 2022; Niazian & Niedbaa, 2020; Rahaman et al., 2019). For example, Yang et al. (2019) developed a convolutional neural network (CNN) classifier to mitigate adulteration in the trade of *Cinnamomum osmophloeum* (var. Kanehira). Similarly, the economic value attributed to heirloom tomatoes requires objective quality assurance in its labeling. Therefore, the primary objective of this research is to develop a classification model based on morphological, color, and physicochemical fruit features to characterize the attributes that exemplify the heirloom market class. In addition, this study aims to determine whether 'heirloom-like' cultivars can meet producers' and consumers' expectations regarding yield and quality. We hope to shed light on the evolving meaning of heirloom and its use as a phenotypic descriptor and assist the breeding community in selecting phenotypes that consumers desire.

Materials & Methods

Plant Material

Solanaceae Coordinated Agriculture Project

To investigate the differences in fruit morphology, color, and physicochemical quality from a diverse sample of cultivars, phenotypic data from the Solanaceae Coordinated Agriculture Project's (SolCAP) vintage (68 accessions) and fresh market (86 accessions) collections were used for this analysis. As part of the cooperative's objectives, standardized phenotypic data were collected to facilitate the identification of fruit quality traits (SolCAP, 2009). SolCAP field trials were structured by pre-defined market classes and conducted in 2009 and 2010 across multiple institutions. Following a preliminary examination to ensure features of interest were recorded during each replicate year, the Ohio State University (OSU) vintage and University of California Davis (UC Davis) fresh market datasets were selected for analysis. Field passports detailing the location, management practices, and experimental designs for the OSU and UC Davis trials are listed in Table 2.1. For each location and year, trials were conducted in a randomized complete block design with three experimental units per plot and replicated twice. Management practices followed the institution's local extension service recommended regional protocols.

Hawai'i Field Trials

To evaluate the fruit morphology, quality, and yield of traditional heirlooms (TH), hybrid heirlooms (HH), and commercial hybrids (CH), field trials were conducted at the University of Hawai'i research stations on Oahu in 2020 and 2021. The field passport data for each location is provided in Table 2.2. Field crops in the tropics encounter significant challenges from pests and diseases. To reduce the severity of pests and diseases, field tests were conducted at each location in high tunnel screen houses. Because the production area was limited to the screen house dimensions, experiments were conducted in an augmented design to maximize genotypes from each market class (Federer & Raghavarao, 1975). Furthermore, the rationale presented by Healy et al. (2015) was adopted, and the number of technical replicates was reduced to include more accessions. An overview of the germplasm screened in each environment and the corresponding seed sources are presented in Table 2.3. Although neither experimental site was certified, the cultural management practices employed during each study followed USDA National Organic Program (NOP) standards.

The first trial was held at the Waimānalo Research Station (21° 20' 7.872" N, 157° 42' 53.2188" W) in a 139 m^2 modified Conley Coldframe (model 1100; Montclair, CA) from August 2020 to January 2021. Seedlings were grown in a greenhouse at the University of Hawaiʻi Mānoa (Honolulu, HI) under organic management practices and treated with a 2% fish emulsion solution (Aqua power [5-1-1]; JH Biotech, Ventura, CA) one week prior to transplanting. The research plot was tilled in July 2020, and five slightly mounded beds (0.9 x 16.8 m^2) were shaped and spaced at 1.5 m centers. The experimental design consisted of five blocks with 55 plots (0.9 x 1.5 m^2), in which four plants were considered an experimental unit. Seven check varieties were completely randomized within each block, and 17 treatment accessions were distributed among all remaining plots. Within row spacing, plants were offset at 60 centimeters apart. A single application of Sustane 8-2-4 (Cannon Falls, MN) was incorporated into each plot at planting to achieve a nitrogen rate of 224 kg/ha. The beds were mulched with wood chips obtained locally and installed with two drip lines. Plants were supported using roller hook lines attached to two overhead high tensile wires running along the bed's perimeter. Indeterminate varieties were grown to a single stem and trained using the ‘lower and lean’ method (See Johnny’s Selected Seeds, 2014), while determinant types were lightly pruned and supported at the primary stem.

Pest management was performed as needed and followed local extension recommendations for organic systems.

A second field trial was conducted at Magoon Research Station (21° 18' 26.748" N, 157° 48' 35.208" W) from June to November 2021. A custom-built screenhouse (92 m^2) was constructed on-site and outfitted with overhead cables to facilitate the ‘lower and lean’ trellising method. Transplants were produced in the same location and managed according to the previous description. The research plot was tilled, and ten slightly mounded beds (0.6 x 5.4 m^2) were shaped at 1.4 m centers. Within row spacing, plants were offset and 51 cm apart. The experimental design comprised five blocks with 36 plots (0.6 x 1.4 m^2) and five plants per experimental unit. Six check varieties were completely randomized within each block, and eight treatment accessions were distributed among all remaining plots. A total fertilization rate of 224 kg/N/ha was provided through a split application of 112 kg/N/ha Sustane 8-2-4 (Cannon Falls, MN) at planting, while the remaining equivalents were supplied through soluble fertilizer (Aqua power [5-1-1]; JH Biotech, Ventura, CA) treatments during flower set and early harvest. All other cultural management and site preparations for the 2020 study were repeated in 2021, with the exception that all genotypes assessed were indeterminate in growth.

Data Collection

Total and Marketable Yield

In each environment, data for yield and marketability were gathered over ten weeks, as established by the initial harvest of each plot. The fruit was harvested as needed to guarantee that specimens for subsequent shape and quality assessments were at their peak maturity. Qualitative assessments to determine marketability were based upon the grading system outlined by Healy et al. (2015). Tomatoes with splitting or insect and disease damage were deemed unmarketable;

however, those with minor cat-facing and dry cracking were considered marketable. Harvest data was recorded per plot (kg/plant/plot), and marketable weights were estimated at each weighing by multiplying the average fruit weight by the number of unmarketable fruits.

Analysis of Tomato Fruit Morphology and Color

Twenty fruits of each accession were harvested at the 'red-ripe' stage, as defined by the USDA grades and standards (USDA, 1991), and analyzed using the Tomato Analyzer (TA v. 4.0) for 42 fruit shape and color metrics. A complete description of TA measures is provided in Table 2.5. A total of ten fruits were prepared for longitudinal and transverse imaging according to the protocol outlined in the TA manual (Gonzalo et al., 2009). Fruit images were captured using an Epson Perfection V39 Color Photo & Document Scanner (Epson America, Inc.; Los Alamitos, CA), and all required calibration procedures were implemented. The average measurements for each fruit per scan were calculated for subsequent analysis.

Evaluation of Fruit Physicochemical Properties

Fruits prepared for TA analysis were examined for the following fruit quality attributes: total titratable acidity (TTA), total soluble solids (reported as degrees Brix %), and pH. Cross-sections of approximately nine fruits were homogenized in a blender, and three 50 mL aliquots were stored at -20 ˚C. Prior to analysis, samples were thawed for four hours in the refrigerator (4 °C) and then brought to room temperature (20–22 °C) (Casals et al., 2019). Each aliquot was re-homogenized and strained with a cheesecloth to remove excess solids. Brix values were estimated using a Sper Scientific digital refractometer (model 30051) with automatic temperature compensation (ATC) (Scottsdale, Arizona) and recorded as the average of three technical replicates. Using the procedures described in Panthee et al. (2013), TTA, estimated as the percent citric acid by volume (% CA), and pH was measured using a Hanna Instruments model 84432

Automatic miniTitrator and pH Meter (Woonsocket, Rhode Island). A detailed summary of the assay protocol is provided in Appendix A.

Data Analysis

All statistical analyses were conducted using the R Statistical Software (version 4.2.0; R Core Team, 2022).

Agronomic Performance of Hawai'i Field Trials

Each environment's total and marketable yield data were calculated as the average kilograms per-plant per-plot (Supplementary Tables 1-6). Due to significant variations across sites, each field experiment was analyzed separately. Total and marketable yields were evaluated by fitting a linear mixed model with genotype as the fixed effects and block as the random effects. The R package 'augmentedRCBD' (Aravind et al., 2015) was used to conduct an analysis of variance (ANOVA) and least square mean comparisons using Fisher's Least Significant Difference (LSD) when $P < 0.05$.

Public Data Mining

Plot means for the 2009 and 2010 SolCAP vintage and fresh market datasets were calculated, and accessions without all three measurement categories (shape, color, and physicochemical quality) were omitted. Before merging the vintage and fresh market datasets, missing data were treated with K-Nearest Neighbor imputation (KNN), where $k = 3$ (R package 'DMwR'; Torgo, 2010). Detailed information regarding the final SolCAP vintage and fresh market accessions used in the classification modeling can be found in Appendix A.

Machine Learning Classifier

Inspired by the methodologies described by Rahaman et al. (2019) and Zou et al. (2019), the following section discusses the techniques used to build a classification model for the heirloom phenotype employing various data mining and ML techniques.

Principal Component Analysis

A principal component analysis (PCA) based on Euclidean distances was used to ascertain the contribution of features to the cumulative variance in 1) the SolCAP vintage and fresh market dataset and 2) the aggregated SolCAP and Hawai'i trial data (R package 'FactoMineR'; Lê et al., 2008). Prior to analysis, all numeric predictors were standardized (z-scores), and the first two principal components were utilized to produce an ordination biplot to assess variable contribution and market class distributions.

Classification Model Comparison

Three supervised ML classification models were evaluated to identify the morphological, color, and physicochemical characteristics that distinguish the heirloom phenotype. Using the conceptual framework proposed in Robnik-Sikonja (2016), a radial basis function network was used to generate 60 synthetic observations from the Hawai'i data (R package 'semiArtificial'; Robnik-Sikonja, 2021). This step was administered to account for potential out-of-distribution error (OOD) when using the model to classify the Hawai'i dataset (Shen et al., 2021). An 80/20 training and validation split, stratifying for market class, was performed on the SolCAP data (including the synthetic observations). See Table 2.4. for details on the dimensions and class representation in the training and validation samples. To perform binary classification, the factor levels for CH and HH were modified to NH (Not Heirloom). Based on Pearson's correlation coefficient ($r > 0.75$), highly correlated variables were omitted during feature selection. The final variables included in the datasets are listed in Table 2.5. Using the methodology described by Chawla et al. (2002), class imbalances (NH= 295; TH= 176) in the training data were corrected with the synthetic minority oversampling technique (SMOTE) (R package ‘Themis’; Hvitfeldt, 2022). All datasets were further preprocessed, including applying the Yeo-Johnson power transformation for numerical predictors and standardizing using z-scores. To identify the optimal ML classifier for the data and classification problem, three models were selected for comparison: 1) Multilayer Perceptron Neural Network (MLPNN), 2) Polynomial Support Vector Machine (SVMP), and 3) Decision Tree (DT) (R package ‘Tidymodels’; Kuhn et al., 2020). Hyperparameters were selected for each model using a grid-search with repeated k-fold (k =5; r = 2) cross-validation (CV). Models were finalized with the selected parameters fit through resampling (CV k = 10; r = 1) to generate performance metrics for ROC-AUC (receiver characteristic operator of the area under the curve), accuracy, specificity, and sensitivity. Information on hyperparameters and model specifications can be found in Table 2.6.

After assessing the preliminary models, the MLPNN was selected for compilation and testing. An additional round of hyperparameter tuning was performed using RStudio’s interface to ‘Keras’ (Allaire & Chollet, 2022) and ‘Tensorflow’ (Abadi et al., 2016). The final network architecture consisted of an input layer with 32 features, and two hidden layers with 32 and 16 neurons, respectively. To prevent overfitting, elastic net regularization was applied to each hidden layer (L1 = 0.0001, L2 = 0.001). The Rectified Linear Unit (ReLU) activation function was employed in the hidden layers, and the sigmoid activation function was applied in the single node output layer. Model training was conducted for 40 epochs, with a batch size of 20, and used the gradient-based Adam optimizer (Kingma and Lei Ba, 2014) with a binary-cross entropy loss function. An out-of-sample error rate was determined using the validation dataset, and accuracy and loss values from the last training epoch were recorded. A summary of the neural network configuration and training parameters can be found in Table 2.7. Binary class predictions (1= Traditional Heirloom, 0= Not Heirloom) and probability estimates were utilized to generate confusion matrices and relevant accuracy statistics for the validation and Hawai'i datasets (R package 'Caret'; Kuhn et al., 2008). Crosstabulations of within-variety predictions for lines screened during the Hawai'i trial were performed to determine the outcomes for the original market class assignments.

A permutation-based test (permutation = 50) was conducted to evaluate the global significance of the individual explanatory variables and their related measurement categories. For each permutation, the area under the ROC curve (AUC) was calculated to estimate the mean 1-AUC impact of each variable on the model's predictive performance. To evaluate feature importance at the local level, SHAP values (Shapely Additive Explanations; Lundberg and Lee, 2017) for a sample of observations from each market class were examined. All post-hoc agnostic tests were performed using R packages in the 'Dr.Why' collection (Biecek & Burzykowski, 2021). Summary statistics by prediction group (NH or TH) were calculated for the 32 fruit measurements (R package 'CompareGroups'; Subirana et al., 2014). The Shapiro-Wilks test was used to assess each variable's normality. For normally distributed variables, the mean and standard deviation (SD) of the prediction groups were calculated, and significant differences between groups were estimated using a one-way analysis of variance (ANOVA) ($P < 0.05$). For non-parametric variables, values are expressed as the median and first and third quartiles, and significant differences between groups were estimated using the Kruskal-Wallis Test ($P < 0.05$).

Results

Hawai’i Field Trials

During the 2020 and 2021 field trials in Hawai’i, 29 cultivars (11 HH, 11 CH, and 6 TH) were tested for total and marketable yield (kg/plant). In the trial conducted at the Waimānalo Research Station in 2020, significant differences were identified for total and marketable yield within and among all sources of variance (Table 2.8). Total yield ranged from 0.32 ± 0.27 to 5.21 ± .64 kg/plant, and marketable yield 0.31 ± 0.25 to 4.95 ± .59 kg/plant. *Skyway*, a commercial hybrid, had the highest values for both yield traits, while *Stealth*, an heirloom hybrid, had the lowest (Table 2.9). For the fruit quality traits TTA and Brix (Figure 2.1), traditional heirlooms' mean TTA (0.56 % CA) was significantly higher than commercial hybrids (P = 5.12e^{-10}) and heirloom hybrids (P = 6.94e^{-8}). There was less variation between class means for Brix, with values for commercial hybrids (3.93%) roughly equivalent to the mean for traditional heirlooms (3.94%). However, whereas traditional heirlooms were more negatively skewed, the distribution for commercial hybrids was positively skewed. Among the market types, commercial hybrids were the only group significantly different (P = 0.03) from heirloom hybrids.

In the second trial, conducted at the Magoon Research Station in 2021, there were significant differences in total and marketable yield for all sources of variation, except for within treatment means (Table 2.10). Adjusted means for total yield ranged from 1.45 ± 0.90 to 9.26 ± .38 kg/plant, and marketable yield 0.87 ± 0.85 to 7.88 ± .36 kg/plant (Table 2.11). The heirloom hybrid *Quasimodo* significantly outperformed all other varieties in the 2021 trial in terms of both yield traits. Although the two trials were not statistically compared, trends were observed for the varieties replicated across environments. The heirloom hybrid *Stealth* had the lowest total yield, which was not statistically different from the observed lowest marketable yield. The traditional heirloom *Old German* was among the highest yielding lines and outperformed the two commercial checks included in the trial. In 2021, mean comparisons for TTA exhibited a comparable ranking among market classes, with traditional heirlooms having the highest mean (0.73% CA) and commercial hybrids the lowest (0.63% CA) (Figure 2.2). Significant differences among the market classes were identified between traditional heirlooms and commercial hybrids ($P = 6.30e^{-3}$) and heirloom hybrids and commercial hybrids ($P = 0.02$). In contrast, while commercial hybrids again had the highest mean Brix (4.34%), no significant differences were identified between the market classes.

Machine Learning Model Comparison

Principal Component Analysis

The SolCAP vintage and fresh market PCA (Figure 2.3.a) identified 76.05% of the total inertia in the first seven principal components (PC), with 42.96% of the cumulative variance explained in the first two dimensions. The first PC, explaining 28.0% of the phenotypic variability, is characterized by eccentricity area index, eccentricity, shoulder height, proximal indentation area, pericarp thickness, circular, fruit shape index external II, proximal blockiness, and TTA (features are listed in descending order of contribution). The second PC was mostly comprised of maximum width, width mid-height, perimeter, proximal angle macro, area, vertical and horizontal asymmetry, and distal blockiness. A two-dimensional plot of PC1-2 and the 20 most significant contributors can be found in Figure 2.3.a. The 95% confidence ellipses reveal a distinct separation between the two market classes, with a minimal overlap occurring in quadrant three associated with fruit shape index measurements.

Combining the SolCAP and Hawai'i phenotypic data sets, the PCA captured 76.86% of the cumulative variance in the first eight dimensions, with PC1-2 accounting for 40.99% (Figure 2.3.b). The features contributing to PC1-2 were comparable to the preliminary results, although their relative contributions varied. The first dimension is associated with the features proximal indentation area, eccentricity area index, shoulder height, eccentricity, and pericarp thickness. The second dimension was also associated with the basic fruit measurements height mid-width, maximum height, and area, although Brix had a greater contribution in PC2 for the SolCAP/Hawai’i data. With the addition of the heirloom hybrid class in Figure 2.3.b, the 95% confidence ellipses for the three market types (TH, CH, and HH) show less distinction than in Figure 2.3.a. However, the distribution for commercial hybrids remains concentrated in quadrant two. Where the ellipses for traditional and hybrid heirlooms overlap, observations are associated with color traits, proximal indentation area, blockiness, and TTA.

Classification Model

Performance metrics were compared for three ML classification models: MLPNN, SVMP, and DT, to identify the optimal classification model. As depicted in Table 2.12, there were marginal differences in precision, ROC-AUC, sensitivity, and specificity across the models. Overall, all benchmark performance metrics were greater than 0.90, with DT having the lowest values compared to SVMP and MLPNN. While the top two models were comparable in terms of ROC-AUC and accuracy, MLPNN was selected due to its superior sensitivity and specificity.

A primary objective of this research was to assess whether ‘heirloom’ can be conceptualized as a phenotypically distinct market class. To address this question, an MLPNN with two hidden units [32:32:16:1] was constructed to identify the morphological, physicochemical quality, and color attributes that distinguish traditional heirloom tomatoes (TH) from modern, hybrid cultivars (HH; CH). The model was trained for 40 epochs, and accuracy and loss values for the validation and training datasets were examined. Results from the final epoch are presented in Table 2.13, and a confusion matrix detailing the prediction statistics for the validation set is provided in Table 2.14. By the final epoch, both datasets achieved high accuracy rates (training 97 %; validation 99 %), which generally indicates a model overfitting the training data (Niazian & Niedbaa, 2020). Based on the convergence and diminishing losses observed in the training and validation datasets, the model was selected to generate market class predictions for the Hawai’i test set. Table 2.15 shows that the model achieved an 85% accuracy rate in classifying the Hawai’i cultivars. While prediction accuracy was greater for the validation data (99 %), this disparity is likely attributed to the heirloom hybrids that make up 40% (n=139) of the testing data. Observations resulting in Type I and Type II errors were examined by computing a cross-tabulation of the Hawai’i cultivars and are arranged by the preassigned market classes (Table 2.16).

The prediction results for the lines assessed during the 2020 and 2021 Hawai'i field trials are reported in Table 2.16 as the proportion of a variety's total technical replicates classified as either TH (Traditional Heirloom) or NH (Not Heirloom). The high specificity (92%) reported is underscored by the fact that all observations for the commercial hybrids were classified under NH (true-negative). Prediction instances for seven heirloom hybrid lines contributed to the models overall Type-I error [*24 Karat* (n=1); *Aurea* (n=1); *Ginfizz* (n=6); *Mai Tai* (n=3); *Marnouar* (n=7); *Quasimodo* (n=5); *Stealth* (n=9)]. However, *Ginfizz, Marnouar,* and *Stealth* were the only heirloom hybrid varieties to receive a majority TH class prediction. Four traditional heirloom varieties contributed to the Type II error [*Ananas Noire* (n=2); *Black Krim* (n=2); *Brandywine* (n=13)], although *Brandywine* was the only one with a majority misclassification. Summary statistics of the 32 fruit measurements estimated for each prediction group (NH or TH) are provided in Supplementary materials (Table 7).

Local and global model agnostics were conducted to examine how the 32 fruit features contributed to the market class predictions. Figure 2.5 illustrates the results of permutation-based feature importance tests for both individual and categorical fruit traits. When subject to 50 permutations, average a value, pH, lobedness degree, average b value, and TTA had the greatest overall impact on prediction error (1-AUC > .025). When features were grouped according to their respective measurement categories, physicochemical, color, distal end fruit shape, blockiness, and latitudinal measurements were the most influential to prediction accuracy (1-AUC > .075).

The mean SHAP values for 25 random orderings were used to estimate the local-additive feature contributions for a sample of varieties from each class. Figure 2.6 compares results for three varieties with red fruit from each market class. Average a value was the most important trait attributed to *Farruco* (CH) and *Quasimodo* (HH), decreasing the TH prediction estimates by -0.09 and -0.16, respectively. The second most important feature reducing *Farruco's* prediction value was pH (z = 0.70), followed by lobedness degree pH (z = -0.49). Average a value also reduced *Costoluto Genovese's (TH) prediction*, but the overall effect was negligible compared to the additive contribution from its attributes in lobedness degree, distal-end protrusion, and TTA. While color parameters reduced *Quasimodo's* prediction, its metrics in perimeter, shoulder height, and TTA increased its predictive estimate. Figure 2.7 shows that, for a replicate of *Quasimodo* that was classified as TH (76%), higher values in lobedness degree and distal blockiness, as well as lower pH, were attributed to its increased predictive value. Figure 2.7 also displays the Shapley values for the three HH cultivars in the experiment that were classified as

TH in most of their technical replicates: *Stealth*, *Ginfizz*, and *Marnouar*. Consistent with the global feature importance test, measurements in physicochemical quality, latitudinal section, and color were attributed to the cultivars' TH classification. Overall, positive z-scores in Brix reduced the TH prediction value, whereas low pH and high TTA values increased the prediction estimate. For the variety *Marnouar*, proximal eccentricity (z = 3.97) contributed the most to TH classification, while distal eccentricity (z = 2.40) was inversely correlated.

Discussion

Since the term first entered common vernacular, the notion of what constitutes as ‘heirloom’ in the fresh market has evolved. Several authors have informally defined heirloom and its related terminology in terms of a cultivar's traceable ancestry, age, and pollination status (Casañas et al., 2017; Male, 1999; Zeven, 1998; Watson, 1996; LeHouillier & Male, 1995). The term heirloom, however, seems to have evolved from previous descriptions as it is now used to describe fruit attributes of novel hybrid cultivars. Prior phenomics studies on the fruit properties in heirloom germplasm have primarily focused on sourcing desirable traits for breeding improvements (Alonso et al., 2011; Dwivedi et al., 2019; Goncalves et al., 2009; Panthee, Labate, McGrath, et al., 2013; Rodríguez-Burruezo et al., 2005). However, there has been no exhaustive examination of ‘heirloom’ as a phenotypic market class. To explore this concept, we developed a supervised ML classifier based on morphology, color, and physicochemical properties to investigate whether the heirloom archetype could be defined. Two field experiments were carried out in Hawai'i as part of this study to evaluate the productivity of cultivars from three market classes (TH, HH, and CH) and determine whether their fruit quality attributes satisfied the requirements for heirloom classification.

We observed significant differences in total and marketable yields (kg/plant) between the three market classes (TH, HH, and CH) in the 2020 and 2021 field trials. Overall, commercial hybrids were among the top performing lines in both yield metrics in 2020 (Waimānalo). The highest yields from this market class were recorded in the three determinate types (*Skyway*, *Cypress*, and *Grebe*) included in the study, suggesting that trellising or pruning techniques may have contributed to the results. Given that phenotypic data collection was the primary objective of this work, we did not restrict the genotypes included to those with disease resistance qualities generally required by local producers (tomato yellow leaf curl (TYLC) and tomato spotted wilt (TSWV). Consequently, an unexpected finding was the strong performance of the TYLC and TSWV susceptible HH variety *Quasimodo*. This variety was the top-performing line in the 2021 (Honolulu) study, and its total and marketable yields in the 2020 trial were not statistically different from those of the top two CH cultivars. Although only 25% of *Quasimodo's* samples were classified as heirloom, we found considerable variation in this variety's fruit samples that may have contributed to both classifications. Considering the variance we observed within several traditional heirloom varieties, it might be argued that the inconsistency within *Quasimodo*'s samples is an 'heirloom-like' quality. *Ginfizz*, one of the three HH varieties that met the classification criteria, was another notable HH variety from the 2021 study that was susceptible to disease yet produced consistent and early yields. As for the other two HH varieties classified as heirloom, *Stealth* and *Marnouar*, neither variety was identified as a top performer. However, *Marnouar* had some of the highest values for TTA and outperformed TH varieties in some cases. As previously stated, environmental conditions were most likely a significant factor in this study; therefore, additional field studies will be required to make sound recommendations to local growers. The traditional heirloom *Old German* provided the most unexpected findings in both field studies, as its total and marketable yields surpassed several commercial hybrids. While the scale and cultural practices used in the field trials may not be representative of more intensive commercial operations, these results suggest that a comparative economic analysis of specialty market types with varying disease resistance may be a fruitful area of research for cooperative extension in Hawai'i.

Using 32 traits related to fruit morphology, color, and physicochemical attributes, we developed an MLPNN classification model that demonstrated high prediction accuracy (85% - 99%) on unseen data. When classifying cultivars from the Hawai'i field trials, it was possible to differentiate between traditional heirlooms, heirloom hybrids, and commercial cultivars with an accuracy rate of 85%. Based on the Hawai'i dataset, it was observed that the model's specificity was greatest for commercial hybrids, as there were no misclassifications for this group. For the TH varieties, prediction sensitivity (true-positive rate) was relatively low (66%); however, this metric must be interpreted with caution given the group's relatively small sample size. Considering that the HH market class accounted for over half (54%) of the observations coded as NH, the negative predictive value (88%) demonstrates the model's ability to distinguish between the heirloom phenotype and observations that may share superficial traits. Based on the prediction results, we can infer that the MLPNN identified a complex set of parameters that distinguishes the heirloom market class. We also found that the misclassification rate for each group was proportional to the size of the classes' 95% confidence ellipse in the PCA plots, with the greatest variance and error occurring for the TH varieties. Conversely, in classifying cultivars from the vintage SolCAP data into nine shape categories, Visa et al. (2014) reported that prediction error and variability within the shape categories were not always correlated. Therefore, using a multinomial model to classify the heirloom phenotype may enhance its robustness to variations within and between TH cultivars. Although the variance may have contributed to the model's error rate, it might be argued that variation within and between heirloom tomatoes is an inherent characteristic that denotes the market type. Moreover, these misclassifications enabled us to make direct comparisons within varieties, offering insights into the relative contribution of specific parameters.

The variable importance tests further corroborated observations that physicochemical quality, color, distal end shape, blockiness, and the latitudinal section were most influential in classifying a fruit sample as an 'heirloom.' Perhaps the most intuitive conclusion drawn from the post-hoc tests is the negative correlation between red fruit (+ average a* value) and the heirloom market type. Given that red tomatoes remain the commercial standard in most markets, the differences in fruit color reflected in heirloom varieties have come to typify the label (Dwivedi et al., 2019; Joseph et al., 2017; Rodríguez-Burruezo et al., 2005). This notion was also conveyed in the classifier, as cultivars with red fruit required a greater additive contribution from other variables, such as high values for lobedness degree, TTA, distal blockiness, or lower values in pericarp area to be identified as heirlooms. One discrepancy which should be noted is the negative z-score for the Brix values associated with heirloom classification in the SHAP tests. While there appears to be a positive association with low values, these results contradict the training data and the findings in Panthee et al. (2013). On closer inspection, it appears that these values stem from the fact that the range for Brix in the Hawai'i data (2.9% to 5.0%) was considerably different from the distribution in the training data (3.0-8.2%). Further investigation will be required to explain this discrepancy; nonetheless, it is probable that the environment influenced the Brix values observed in the field studies. Evidence supporting that high TTA is associated with the class was more conclusive and consistent with the study previously cited.

According to the HH varieties that met the classification requirements, low values in the pericarp area may be a unifying characteristic. This feature was also reflected in misclassified samples of the TH variety *Brandywine.* The model's relative weights for color parameters and lobedness degree may have detracted from the importance of other pertinent phenotypic traits identified in the heirloom germplasm. A correction for biases in fruit color would be beneficial in future applications to extend insights for classification based on morphology and physicochemical properties.

Conclusion

This study represents a first attempt to address classifying heirloom as a phenotypic market class. The methodology presented appears to be quite promising for creating a measurable definition for contextualizing the heirloom market type; however, the generality of the classification model must be established through future research. Although measuring the chemical composition and perception of flavor was outside the scope of this study, it represents an intriguing area for future research and remains an essential element required to define the heirloom archetype. The implications of this field of study may provide a spectrum of desirable traits that can be targeted in future breeding programs, broaden the definitions of what makes a cultivar heirloom, and enhance ongoing efforts to improve fresh market tomato quality.

Chapter 2. Tables

Table 2.1. SolCAP field passports for the 2009 and 2010 Ohio State University (OSU) vintage and University of California Davis (UC Davis) fresh market phenotyping studies.

Institute	**University of California Davis**	**Ohio State University**
Market class	Fresh Market	Vintage
Location	Davis, CA	Fremont, OH
*Number of Accessions**	144	84
Experimental Design	RCBD (Two replications x Year)	RCBD (Two replications x Year)
Management	Each institute followed regional extension recommendations.	

* Number of accessions reflects the dataset prior to preprocessing and analysis.

Table 2.2. Field passport for two field trials conducted in Hawai’i during 2020 and 2021.

	Field TRIAL 2020	**Field TRIAL 2021**
Location	Waimānalo Research Station	Magoon Research Station
GPS Coordinates	21° 20' 7.872" N 157° 42' 53.2188" W	21° 18' 26.748" N 157° 48' 35.208" W
Elevation (m/Asl)	24	50
Name Of Farm or Institute	The University of Hawaiʻi at Mānoa	
Street Address	41-698 Ahiki St, Waimānalo, HI 96795	2727 Woodlawn Dr, Honolulu, HI 96822
Year	2020-2021	2021-2022
Transplanting Date	8/7/2020 - 9/15/2020	6/29/2021
First Harvest Date	10/2/2020-11/16/2020	8/21/2021-8/25/2021
Last Harvest Date	10-week harvest period	
Annual Rainfall (mm)	1397	3846
Annual Temperature (Minimum-Maximum °C)	20-28	21-24
Soil Description	Waialua, Very-fine, mixed, superactive, isohyperthermic Pachic Haplustolls	Makiki, fine, mixed, active, isohyperthermic Typic Haplustepts
Texture	Silty clay	Clay loam
Management Practices	Followed local extension service recommendations. Utilized organic management practices, although the site was not NOP certified.	
Experimental Design	RCBD Augmented Design (Federer & Raghavarao, 1975)	

Table 2.3. Description of germplasm screened in two Hawai'i field trials conducted from 2020 to 2021.

Waimānalo 2020

Seed Source	Entry Name	Market Class
NeSeeds	*Brandywine Pink*	TH
NeSeeds	*Black Krim*	TH
NeSeeds	*Old German*	TH
NeSeeds	*Costoluto Genovese*	TH
NeSeeds	*Dr. Wyche's Yellow Beefsteak*	TH
NeSeeds	*Pamela*	CH
NeSeeds	*Shining Star*	CH
Paramount	*24 Karat*	HH
Paramount	*Pink Smart*	HH
Paramount	*WS-2507*	CH
Paramount	*WS-2519*	CH
Paramount	*Stealth*	HH
Paramount	*Eto Truss*	HH
Paramount	*Aurea*	HH
Paramount	*Grebe*	CH
Paramount	*Quasimodo*	HH
Yuksel Tohum	*Farruco*	CH
Yuksel Tohum	*Nemesis*	CH
Yuksel Tohum	*Gelidonya*	CH
Yuksel Tohum	*Eurasia*	CH
Seminis	*Cypress*	CH
Johnny's Select Seed	*Skyway*	CH

Honolulu 2021

Seed Source	Entry Name	Market Class
NeSeeds	*Brandywine Pink*	TH
NeSeeds	*Old German*	TH
NeSeeds	*Costoluto Genovese*	TH
NeSeeds	*Pamela*	CH
Paramount	*Pink Smart*	HH
Paramount	*Stealth*	HH
Paramount	*Quasimodo*	HH
Yuksel Tohum	*Farruco*	CH
Johnny's Select Seed	*Marnouar*	HH
Johnny's Select Seed	*Marsalato*	HH
Harris Seed	*Ginfizz*	HH
Harris Seed	*Mai tai*	HH
Tomato Fest	*Ananas Noire*	TH
Cornel University	*Brandywise*	HH

Table 2.4. The sample size, market class demographics, and data sources for the training, validation, and Hawai'i datasets used to develop and test the Multilayer Perceptron Neural Network (MLPNN) classifier.

		Class Count	
Dataset	***Sample Size***	**TH – CH - HH**	***Data Source***
Training	N = 528	210– 305 – 15	SolCAP (90%) - Synthetic HI (10%)
Validation	N = 132	54 – 77 – 1	SolCAP (95%) - Synthetic HI (5%)
HI Testing	N = 345	82 – 124 – 139	HI (100%)

Table 2.5. The Tomato Analyzer (TA) measurements for fruit shape and color features organized according to the measurement categories described in the TA (v. 4.0) user manual. The measurements described here have been adapted from those reported in Darrigues et al. (2008) and Ramos et al. (2018).

Measurement Category	**Measurement (cm)**	**Description**
Basic Measurements	Perimeter*	Total distance around the fruit boundary.
	Area	Total area enclosed by the fruit boundary.
	Width Mid-height	Width measured at half of the fruit's height.
	Maximum Width	Maximum horizontal distance of the fruit.
	Height Mid-width	Height measured at half of the fruit's width.
	Maximum Height*	Maximum vertical distance of the fruit.
Fruit Shape Index	Fruit Shape Index External I*	Ratio of the maximum height to maximum width.
	Fruit Shape Index External II	Ratio of height mid-width to width mid-height
Blockiness	Proximal Fruit Blockiness	Ratio of fruit width at the proximal end to mid-width
	Distal Fruit Blockiness*	Ratio of fruit width at the distal end to mid-width.
	Fruit Shape Triangle*	Ratio of proximal width to distal width.
Homogeneity	Ellipsoid	Error ratio from best-fit ellipse to fruit area. Error is the average residuals along the fruit's perimeter divided by the ellipse's major axis. Smaller values indicate more ellipsoid fruit.
	Circular	Error ratio from best-fit ellipse to fruit area. Error is the average residuals along the fruit's perimeter divided by the radius of the circle. Smaller values indicate more circular fruit.
	Rectangular*	Ratio of the area of the rectangle bounding the fruit to the area of the rectangle bounded by the fruit.
Proximal Fruit End Shape*	Shoulder Height	The ratio of the average height of the shoulder points above the proximal endpoint to maximum height.
	Proximal Angle Micro	The angle between best-fit lines drawn through the fruit perimeter on either side of the proximal endpoint. Micro setting: points comprising 1% of the perimeter on either side of that center point used in the regression.
	Proximal Angle Macro	(See above) Macro setting: points comprising 5% of the perimeter on either side of that center point used in the regression.

	Proximal Indentation Area	The ratio of the area of the proximal indentation (bounded by the proximal shoulder points) to the total area of the fruit (x10).
Distal Fruit End Shape*	Distal Angle Micro	The angle between best-fit lines drawn through the fruit perimeter on either side of the distal endpoint. Micro setting: points comprising 1% of the perimeter on either side of that center point used in the regression.
	Distal Angle Macro	(See above) Macro setting: points comprising 5% of the perimeter on either side of that center point used in the regression.
	Distal Indentation Area	The ratio of the area of the distal indentation (bounded by the distal protrusion points) to the total area of the fruit (x10).
	Distal End Protrusion	The ratio of the area of the distal protrusion (bounded by the distal protrusion points) to the total area of the fruit (x10).
Asymmetry*	Obovoid	Describes the degree to which the fruit is bottom-heavy.
	Ovoid	Describes the degree to which the fruit is top heavy.
	V. Asymmetry	Average distance between a vertical line through the fruit at mid-width and the midpoint of the fruit's width at each height.
	H. Asymmetry Ob.	If the area of the fruit is greater below mid-height than above it, measures the average distance between a horizontal line through the fruit at mid-height and the midpoint of the fruit's height at each width. Otherwise, it is 0.
	H. Asymmetry Ov.	If the area of the fruit is greater above mid-height than below it, measures the average distance between a horizontal line through the fruit at mid-height and the midpoint of the fruit's height at each width. Otherwise, it is 0.
	Width Widest Pos.	Ratio of the height at which the maximum width occurs to the maximum height.
Internal Eccentricity	Eccentricity	Ratio of the height of the internal ellipse to the maximum height.
	Proximal Eccentricity*	Ratio of the height of the internal ellipse to the distance between the bottom of the ellipse and the top of the fruit.
	Distal Eccentricity*	Ratio of the height of the internal ellipse to the distance between the top of the ellipse and the bottom of the fruit.
	Fruit Shape Index Internal	Ratio of the internal ellipse's height to its width.
	Eccentricity Area Index	Ratio of the area of the fruit outside the ellipse to the total area of the fruit.
Latitudinal Section	Lobedness Degree*	The degree of uneven shape, measured by the standard deviation of the lengths between each boundary point and the weight center.
	Pericarp Area*	The area between the pericarp boundary and the perimeter.
	Pericarp Thickness	The pericarp area divided by the average of the length of the pericarp boundary and the perimeter

Average Color Values* *CIELab color space*	a	Chromacity coordinate, where +a* is the red direction and -a* is the green direction.
	b	Chromacity coordinate, where +b* is the yellow direction and –b* is the blue direction
	L	Vertical axis of color space indicating lightness (+L*) to darkness (-L*)
	Chroma	Describes the saturation of the color, measured radially from the center of each quadrant with the a* and b* axes.
	Luminosity	The average luminosity across all pixels, calculated from the RGB value of each pixel [(max(R, G, B) + min(R, G, B)) * 240] / (2 * 255)
	Hue	Represents the basic color, estimated as the angular measurement in the quadrant between the a* and b* axes

**Features included in the final datasets used to train the classification model. If indicated in the measurement category, all features are included.*

Table 2.6. A summary of the hyperparameters derived from a grid search with 10-fold cross-validation for three machine learning (ML) models: Multilayer Perceptron Neural Network (MLPNN), Support Vector Machine using a Polynomial kernel function (SVMP), and Decision Tree (DT).

Classifier [R package]	***Hyperparameters***
MLPNN* [Keras]	Hidden Layer = 1 Hidden Units = 16 Dropout Rate = 0.01 Epochs = 50 Activation Function = ReLu
SVMP [Kernlab]	Cost = $0.01e^{-1}$ Degree of Interaction = 3 Scale Factor = 0.09 Insensitivity Margin = $1.23e^{-1}$
DT [Rpart]	Minimal Node Size = 30 Cost Complexity = $1.60e^{-5}$

*****Machine learning (ML) model selected. For the final MLPNN architecture used in training, see Table 2.7.

Table 2.7. The final network architecture [32:32:16:1] and training parameters used to construct the Multilayer Perceptron Neural Network (MLPNN) classifier.

Layer Type	***Output Shape***	***Parameter Count***
Dense - 1	(None, 32)	1056
Dense - 2	(None, 16)	528
Output	(None, 1)	17

Total parameters: 1,601
Trainable parameter: 1,601
Non-trainable parameters: 80

Training parameters: epochs =40; batch-size = 20

Table 2.8. Analysis of Variance (ANOVA) for block and treatment adjusted total and marketable yields (kg/plant) in the Waimānalo 2020 field trial.

Treatment Adjusted

Source of Variation	*Df*	*Marketable Yield (kg/plant)*	*Total Yield (kg/plant)*
Block (Ignoring Treatments)	4	3.51 **	4.74 **
Treatment (Eliminating Blocks)	22	2.30 **	2.47 **
Treatment: Check	6	1.50 **	1.91 **
Treatment: Test and Test vs. Check	16	2.60 **	2.68 **
Residuals	24	0.32	0.37
Block Adjusted			
Treatment (Ignoring Blocks)	22	2.72 **	3.01 **
Treatment: Check	6	1.50 **	1.91 **
Treatment: Test vs. Check	1	11.54 **	12.55 **
Treatment: Test	15	2.62 **	2.81 **
Block (Eliminating Treatments)	4	1.20 *	1.77 **
Residuals	24	0.32	0.37

ns $P > 0.05$; * $P < 0.05$; ** $P <= 0.01$

Table 2.9. Estimated marginal means for total and marketable yield for the Waimānalo 2020 field trial. Pairwise comparisons were computed using Fisher's Least Significant Difference (LSD; $P < 0.05$).

Treatment	*Market Class*[2]	*Marketable Yield (kg/plant)*	*Total Yield (kg/plant)*
Cypress	CH	4.95 a	5.16 a
Skyway	CH	4.95 a	5.21 a
Quasimodo	HH	4.38 a	4.37 ba
Grebe	CH	3.81 ba	4.21 ba
Old German	TH	2.23 cb	2.30 dc
Espresso	HH	2.15 cb	2.30 dc
Eurasia	CH	2.13 cb	2.92 cb
Farruco	CH	1.71 c	2.01 dc
Nemesis	CH	1.65 dc	1.93 edc
Pamela	CH	1.60 c	1.73 dc
Shining Star	CH	1.60 c	1.91 dc
Aurea	HH	1.35 edc	1.28 fedc
WS-2519	CH	1.33 edc	1.50 fedc
Gelidonya	CH	1.33 c	1.55 edc
24-Karat	HH	1.18 dc	1.44 ed
Dr. Wyche's Yellow Beefsteak	TH	1.15 edc	1.46 edc
Brandywine	TH	1.14 edc	1.92 edc
WS-2507	CH	1.01 edc	1.07 fedc
Eto Truss	HH	1.01 edc	1.17 fedc
Costoluto Genovese	TH	0.89 edc	1.05 fedc
Black Krim	TH	0.55 ed	0.79 fe
Pink Smart	HH	0.52 edc	0.61 fed
Stealth	HH	0.31 e	0.32 f

[1] Letter notation shared among values not significantly according to Fisher's Least Significant Difference (LSD) ($P < 0.05$). Means comparisons are relative to the respective column's trait.

[2] Market class abbreviations: Commercial Hybrid (CH); Heirloom Hybrid (HH); Traditional Heirloom (TH).

Table 2.10. Analysis of Variance (ANOVA) for block and treatment adjusted total and marketable yields (kg/plant) in the Honolulu 2021 field trial.

Treatment Adjusted			
Source of Variation	***Df***	***Marketable Yield (kg/plant)***	***Total Yield (kg/plant)***
Block (Ignoring Treatments)	4	2.96 **	2.66 *
Treatment (Eliminating Blocks)	13	10.83 **	14.84 **
Treatment: Check	5	23.48 **	34.18 **
Treatment: Test and Test vs. Check	8	2.91 **	2.76 **
Residuals	20	0.64	0.71
Block Adjusted			
Treatment (Ignoring Blocks)	13	10.97 **	14.87 **
Treatment: Check	5	23.48 **	34.18 **
Treatment: Test vs. Check	1	18.22 **	13.73 **
Treatment: Test	7	0.99 ns	1.24 ns
Block (Eliminating Treatments)	4	2.50*	2.58 *
Residuals	20	0.64	0.71

ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$

Table 2.11. Estimated marginal means for total and marketable yield for the Honolulu 2021 field trial. Pairwise comparisons were computed using Fisher's Least Significant Difference (LSD;P<0.05).

Treatment	***Market Class[2]***	***Marketable Yield (kg/plant)***	***Total Yield* (kg/plant)**
Quasimodo	HH	7.88 a	9.26 a
Ginfizz	HH	4.64 cb	4.75 dcb
Old German	TH	4.54 b	5.12 b
Pamela	CH	3.34 dc	3.58 dc
Farruco	CH	3.32 dc	4.20 dcb
Pink Smart	HH	2.94 dc	3.16 ed
Marsalato	HH	2.57 edc	3.17 fedcb
Mai Tai	HH	2.57 edc	5.27 cb
Brandywine	TH	2.52 edc	3.09 fedcb
Costoluto Genovese	TH	2.02 ed	2.29 fed
Ananas Noire	TH	1.67 ed	2.34 fed
Marnouar	HH	1.52 e	1.60 f
Stealth	HH	1.49 ed	1.45 fe
Brandywise	HH	0.87 e	2.44 fed

[1] Letter notation shared among values not significantly according to Fisher's Least Significant Difference (LSD) ($P < 0.05$). Mean comparisons are relative to the respective column's trait.

[2] Market class abbreviations: Commercial Hybrid (CH); Heirloom Hybrid (HH); Traditional Heirloom (TH).

Table 2.12. Results for accuracy, ROC-AUC, sensitivity, and specificity for three classification models: Support Vector Machine (SVM) using a polynomial kernel function, Multilayer Perceptron Neural Network (MLPNN), and Decision Tree (DT). Metrics are expressed as the mean ± standard error prediction values computed from 10-fold cross-validation (CV).

	Machine Learning Models		
***Metrics*[1]**	**SVM Polynomial**	**Multilayer Perceptron Neural Network**	**Decision Tree**
Accuracy	$.96 \pm 6.4e^{-3}$	$.96 \pm 4.1e^{-3}$	$.94 \pm 1.1e^{-2}$
ROC-AUC	$.99 \pm 3.3e^{-3}$	$.99 \pm 4.9e^{-3}$	$.97 \pm 8.7e^{-3}$
Sensitivity	$.97 \pm 3.3e^{-3}$	$.98 \pm 6.1e^{-3}$	$.97 \pm 7.5e^{-3}$
Specificity	$.94 \pm 1.1e^{-2}$	$.95 \pm 1.1e^{-2}$	$.91 \pm 2.5e^{-2}$

[1] Values expressed as the mean ± standard error from resampling (10-fold CV)

Table 2.13. Prediction accuracy and optimization loss for the training and validation datasets. Accuracy and loss reflect the values computed in the final training epoch for a Multilayer Perceptron Neural Network (MLPNN) classifier.

Final Epoch Results		
Dataset	**Loss**	**Accuracy**
Training set	0.04	0.97
Validation set	0.03	0.99
Training parameter: Epochs=40; Batch-size=20		

Table. 2.14. Confusion matrix and classification statistics generated from the validation dataset predictions.

Confusion Matrix			Prediction Statistics
	Prediction		**Accuracy -** 0.99
Truth	NH	TH	**95% Confidence Interval:** [0.96, 1.00]
NH	78	0	**No Information Rate (NIR):** 0.60
TH	1	53	**P-Value [ACC > NIR]:** < 2.0 e^{-16}
			Kappa: 0.98
			McNemar's Test P-Value: 1
			Sensitivity: 1.00
			Specificity: 0.99
			Positive (TH) Prediction Value: .98
			NH Prediction Value: 1.00
			Prevalence: 0.40
			Detection Rate: 0.40
			Detection Prevalence: 0.41
			Balanced Accuracy: 0.99

Table. 2.15. Confusion matrix and classification statistics generated from the Hawai'i dataset predictions.

Confusion Matrix			Prediction Statistics
	Prediction		**Accuracy -** 0.85
Truth	NH	TH	**95% CI:** [0.80, 0.88]
NH	231	32	**No Information Rate (NIR):** 0.73
TH	21	61	**P-Value [ACC > NIR]:** 2.08e^{-7}
			Kappa: 0.59
			McNemar's Test P-Value: 0.17
			Sensitivity: 0.66
			Specificity: 0.92
			Positive) Prediction Value: 0.74
			NH (Negative) Prediction Value: 0.88
			Prevalence: 0.27
			Detection Rate: 0.18
			Detection Prevalence: 0.24
			Balanced Accuracy: 0.79

Table 2.16. A summary of predicted market types for each cultivar studied in the 2020 and 2021 field trials in Hawai'i. The proportions for each prediction group (NH = Not Heirloom; TH = Traditional Heirloom) correspond to the total number of technical replicates for each variety. Bold and underlined values indicate the market class with the highest prediction count (n 50%) for each variety.

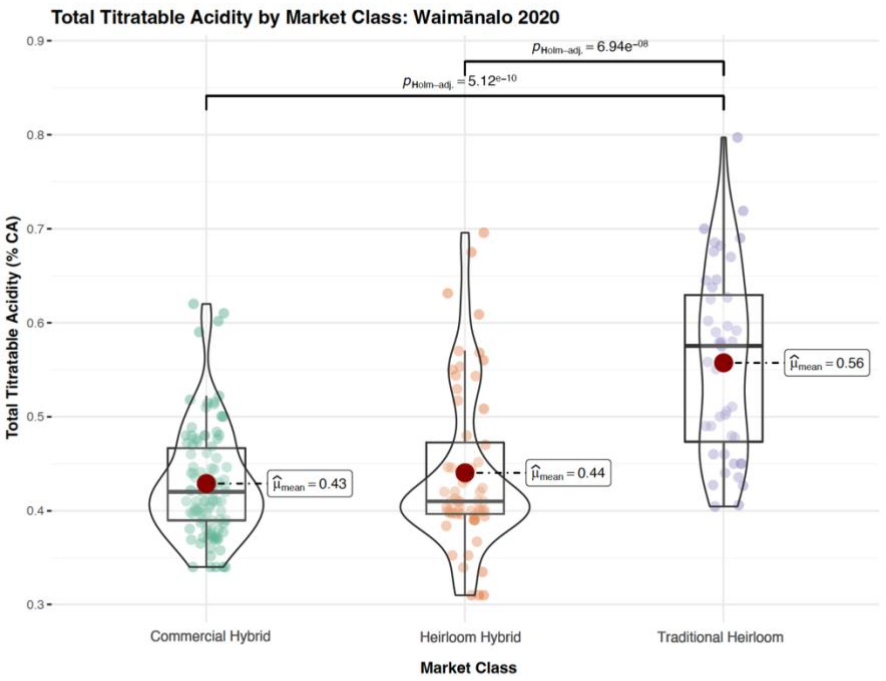
		Predictions n (%)[1]	
Market Class	**Variety**	**True Heirloom**	**Not Heirloom**
Commercial Hybrid	*Cypress*	0 (0%)	**9 (100%)**
	Eurasia	0 (0%)	**5 (100%)**
	Farruco	0 (0%)	**24 (100%)**
	Gelidonya	0 (0%)	**12 (100%)**
	Grebe	0 (0%)	**10 (100%)**
	Nemesis	0 (0%)	**11 (100%)**
	Pamela	0 (0%)	**21 (100%)**
	Shining Star	0 (0%)	**11 (100%)**
	Skyway	0 (0%)	**11 (100%)**
	Ws-2507	0 (0%)	**5 (100%)**
	Ws-2519	0 (0%)	**5 (100%)**
Heirloom Hybrid	*24 Karat*	1 (8%)	**12 (92%)**
	Aurea	1 (10%)	**9 (90%)**
	Brandywise	0 (0%)	**6 (100%)**
	Espresso	0 (0%)	**10 (100%)**
	Eto Truss	0 (0%)	**9 (100%)**
	Ginfizz	**6 (60%)**	4 (40%)
	Mai Tai	3 (30%)	**7 (70%)**
	Marnouar	**7 (70%)**	3 (30%)
	Marsalato	0 (0%)	**10 (100%)**
	Pink Smart	0 (0%)	**14 (100%)**
	Quasimodo	5 (25%)	**15 (75%)**
	Stealth	**9 (53%)**	8 (47%)
Traditional Heirloom	*Ananas Noire*	**6 (75%)**	2 (25%)
	Black Krim	**9 (82%)**	2 (18%)
	Brandywine	7 (35%)	**13 (65%)**
	Costoluto Genovese	**14 (78%)**	4 (22%)
	Dr. Wyche's Yellow Beefsteak	**5 (100%)**	0 (0%)
	Old German	**20 (100%)**	0 (0%)

[1]Values **bold and underlined** indicate the majority class prediction (n ≥ 50%) for each variety.

Chapter 2. Figures

Figure 2.1. Mean comparison between Waimānalo 2020 market class values using the Games-Howell test (Holmes adjusted $P < 0.05$) for two fruit quality traits: (a) Total Titratable Acidity (TTA; % Citric Acid) and (b) Degrees Brix.

(a)



(b)

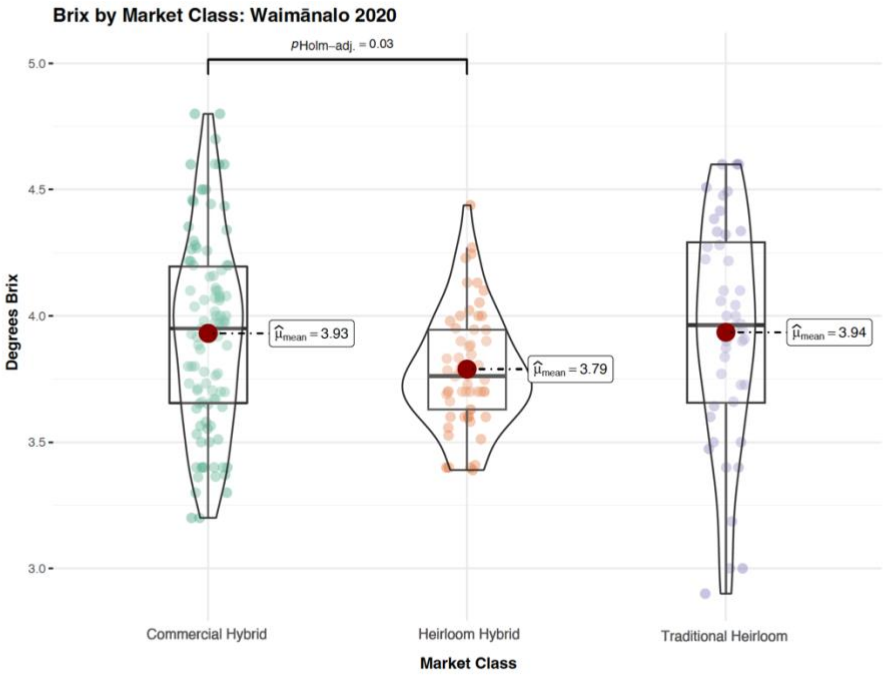


Figure 2.2. Mean comparison between Honolulu 2021 market class values using the Games-Howell test (Holmes adjusted $P < 0.05$) for two fruit quality traits: (a) Total Titratable Acidity (TTA) and (b) Degrees Brix.

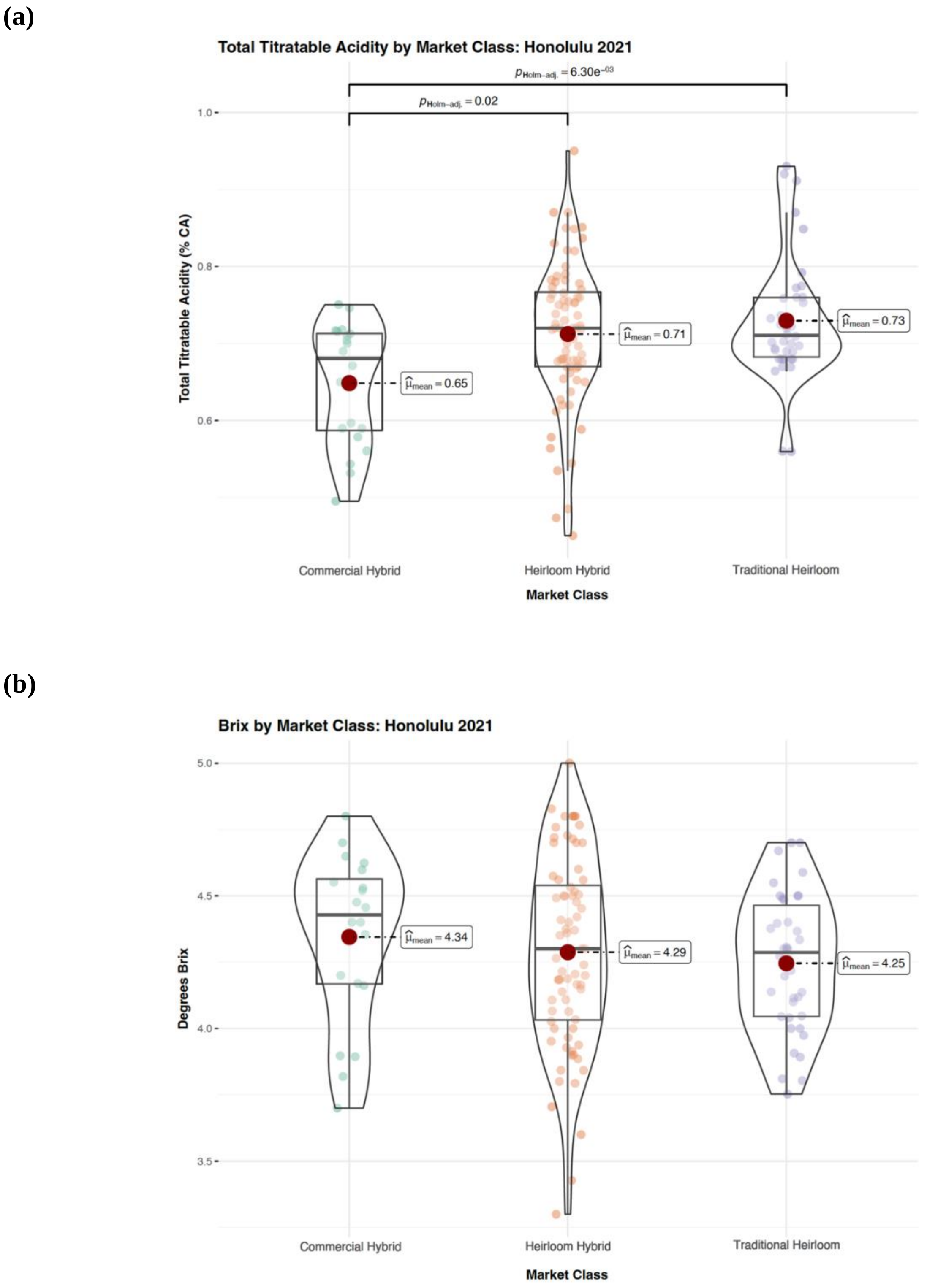


Figure 2.3. Ordination bi*p*lots for two Principal Component Analyses (PCA) obtained from 48 fruit measurements representing morphological, color, and physicochemical properties. (A) PCA results for the SolCAP vintage and market-fresh accessions. The axis represents the first two principal components (PC), which account for 43.0% of the cumulative variance. (B) PCA results for the SolCAP and 2020-2021 Hawai'i data. The axis depicts the first two PCs and captures 41.0% of the cumulative variance. The top 20 features contributing to the variance in PC 1-2 are plotted in each biplot, and 95% confidence ellipses denote each market class.

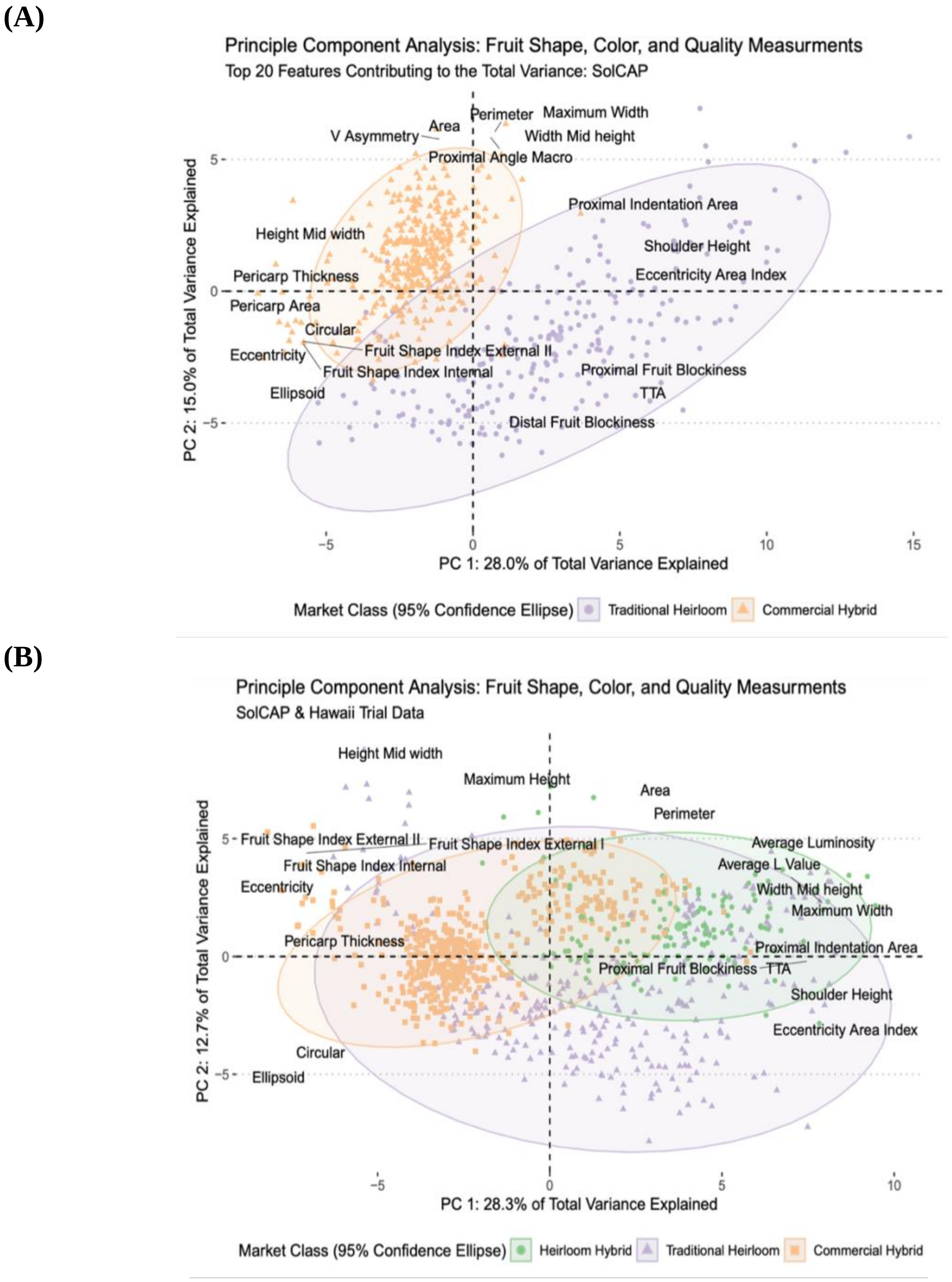


Figure 2.5. Variable importance estimated from individual and categorical fruit feature permutations. Feature importance is estimated from the mean prediction error (1-AUC) after 50 iterations of feature permutation.

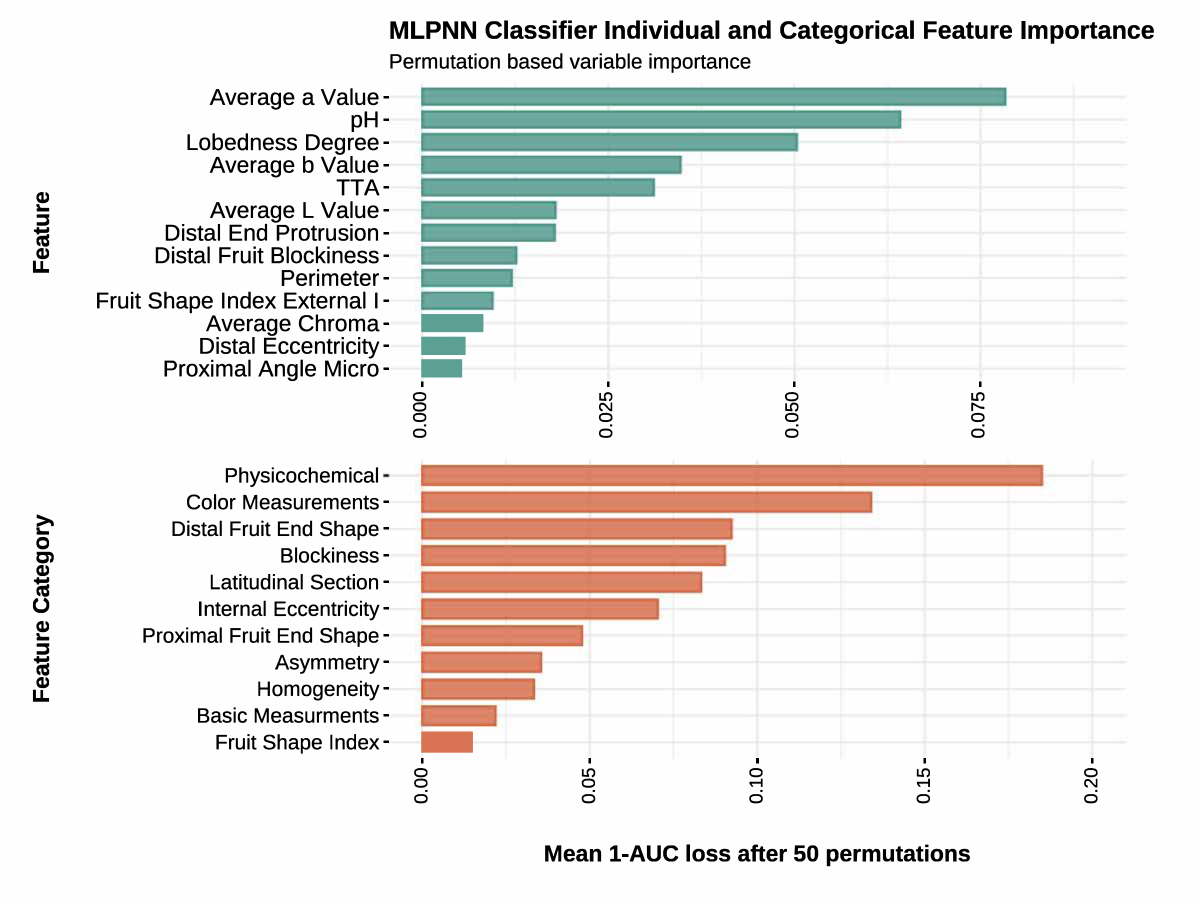


Figure 2.6. Shapley additive explanation (SHAP) for a commercial hybrid (CH), heirloom hybrid (HH), and traditional heirloom (TH). From top to bottom: Farruco, Quasimodo, and Costoluto Genovese. Additive contributions were computed separately for each variety and were estimated as a feature's mean contribution from 25 random feature orderings. Graphs illustrate the top ten features identified for each observation. The blue and red bars reflect whether the observed values contributed positively or negatively to the cumulative TH prediction probability [0,1].

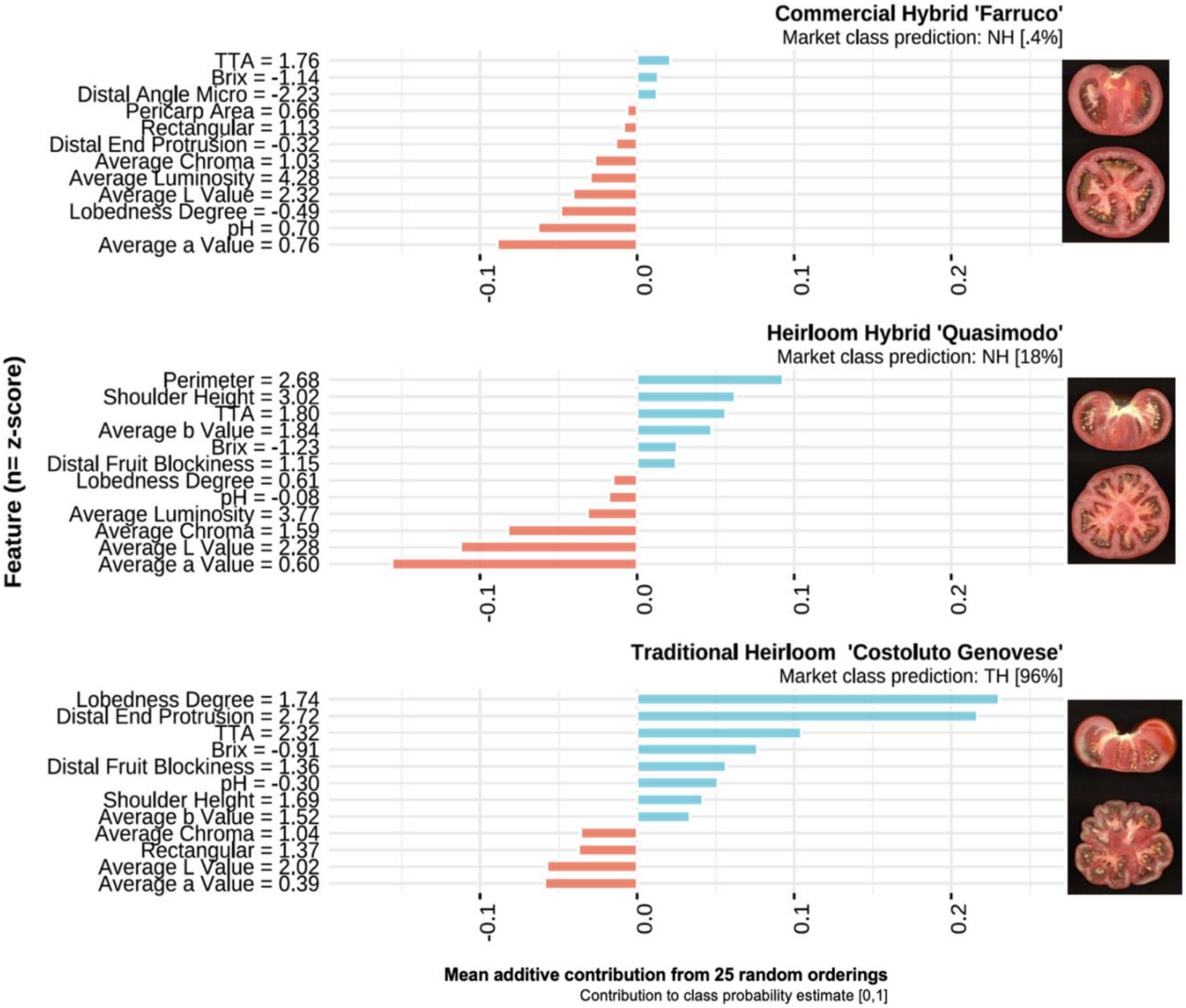
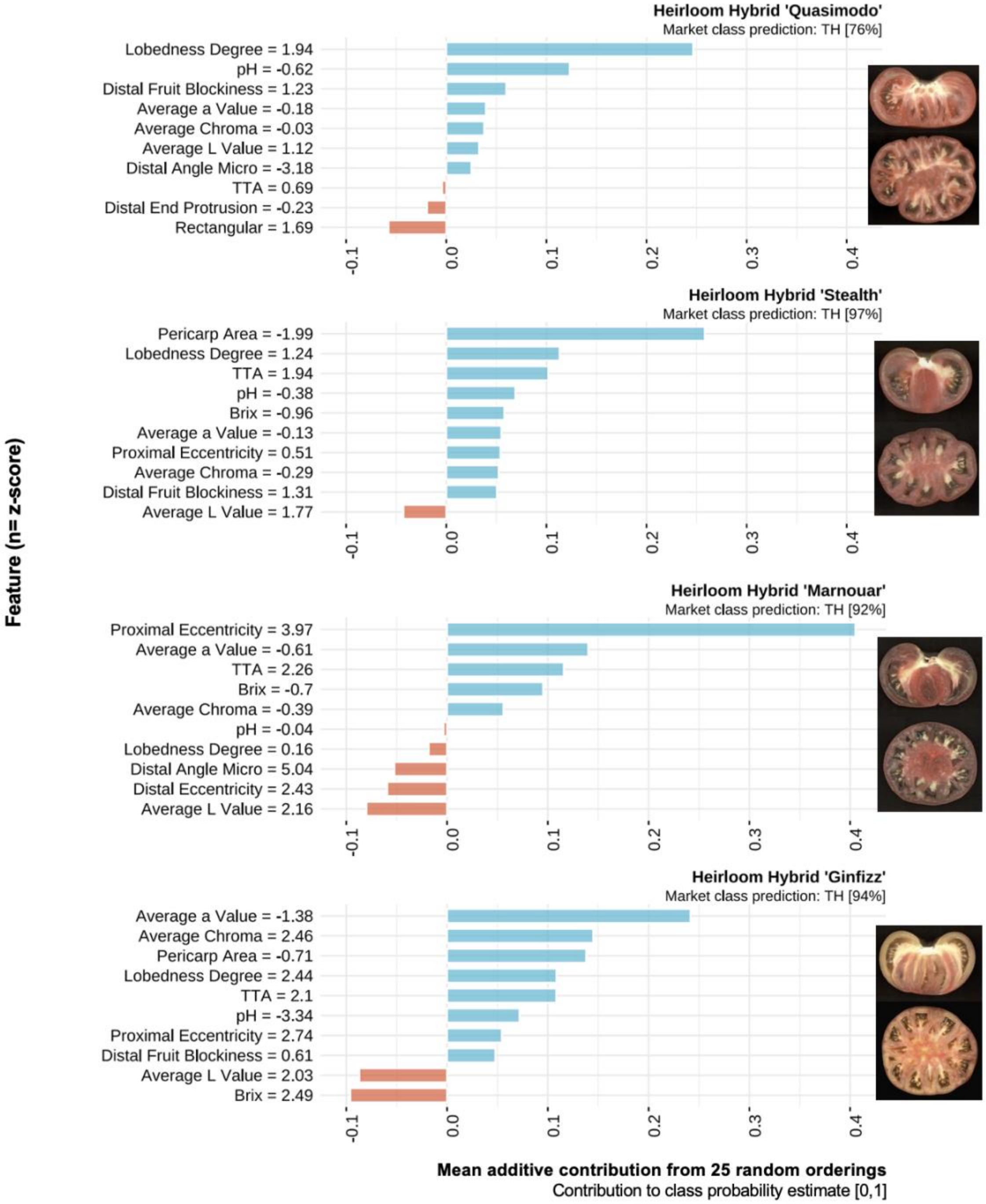


Figure 2.7. Shapley additive explanations for a sample of heirloom hybrid (HH) cultivars classified as traditional heirlooms (TH). From top to bottom: *Quasimodo, Stealth*, *Marnouar*, and *Ginfizz.* Additive contributions were computed separately for each variety and were estimated as a feature's mean contribution from 25 random feature orderings. Graphs illustrate the top ten features identified for each observation. The blue and red bars reflect whether the observed values contributed positively or negatively to the cumulative TH prediction probability [0,1].



Chapter 3. Moving Heirlooms Forward into the Future

Heirloom tomatoes have come to personify the preferred fresh market archetype and command a substantial premium in the marketplace. Although prior definitions of 'heirloom' are informal and vary across synonyms, the term’s use in describing fruit attributes in modern cultivars have wholly deviated from established concept. Given that assertions of 'heirloom-like' features lack a standardized context for comparisons, many of these claims are currently anecdotal. This thesis employed two approaches to investigate distinctions between heirloom and modern cultivars: (1) Two field trials comparing production and quality across different environments in Hawai'i, and (2) incorporating high-throughput phenotyping and machine learning to examine prominent fruit features that can be used to define an ‘heirloom’ ideotype for fresh market tomatoes.

As expected, many distinctive traits of heirloom fruit, such as color, lobedness degree, fruit size (perimeter), and blockiness, are visible cues typically marketed to consumers. The fact remains, however, that customers cannot discern between products based on the quality of their internal components, such as chemical composition and pericarp thickness. This is especially relevant in the context of ‘Neo-heirlooms.' If a tomato has the exterior traits of an heirloom and may even be labeled as such, but lacks the intrinsic quality that customers anticipate, this presents a significant ethical concern regarding heirloom labeling. Consumer demand for heirloom tomatoes is reflected in their high market value (Alexander, 2006; Gertner, 2004). The price attributed to traditional heirloom varieties can also reflect the substantial risk growers undertake in producing varieties that typically lack the yield or disease resistance of modern hybrids (Klee & Tieman, 2018; Sydorovych et al., 2013). As previously discussed, (see chapter one), the historical and contemporary perspectives on what constitutes an heirloom, landrace, or heritage variety are dominated by a dual ethos. The plights for conservation and seed sovereignty by the *Seed Saver's Exchange* reflect a definition of heirloom based on social and cultural ethics. On the other hand, there is the heirloom tomato which is featured in culinary magazines and sold for roughly $6 per pound in artisanal grocery stores. Though it might be argued that the latter is linked with adverse notions of consumerism, these two identities are united in connotating 'heirloom' with local food systems and superior sensory quality. Although post-harvest handling and shelf life were not explicitly investigated in this thesis, they are crucial factors that affect fruit quality and have also influenced the heirloom tomato's historical perceptions. Small, low-input production systems have been the primary source of traditional heirloom tomatoes, with many growers relying on direct-market sales to ensure optimal harvest and distribution timing. A critical area to broach is the role of the cultural practices used to produce cultivars that fall within the heirloom market type. If 'Neo-heirlooms' are to penetrate the market and warrant the price premiums associated with their label, it will be imperative that they do not perpetuate the quality issues associated with mass production.

This research demonstrated that the heirloom ideotype can be targeted by selecting specific phenotypic qualities; however, to retain the integrity and value of the label, the heirloom market type should be appraised based on the merits of the end product's quality. Certification policies like the National Organic Program (NOP) in the U.S. (AMS-USDA, 2022) and Quality Labeling in the European Union (European Commission, 2019) represent possible solutions to protect growers and ensure quality control in the heirloom market. Several researchers have described this theoretical approach for European landraces (Pérez-Caselles et al., 2020; Petropoulos et al., 2019; Romero del Castillo et al., 2021; Skreli et al., 2017), with many indicating that the benefits of Quality Labels, particularly the Protected Designation of Origin (POG), Protected Geographical Indication (PGI), and Traditional Specialties Guaranteed (TSG), primarily benefited small farmers. Traditional seeds developed and maintained by families, communities, or religious groups may require additional regulations and certification to ensure their preservation and cultural significance.

While discussions over what constitutes heirloom germplasm will continue, steps towards incorporating consumer quality and the success of small farmers can integrate historical components of the heirloom tomato in future cultivars. Alternative methods for cultivar development should be explored in the public sector to achieve these objectives. Participatory Plant Breeding (PPB) offers a framework for establishing and preserving 'heirloom' as a high-quality market type by involving consumers and producers in the breeding process. This method has been successfully used to breed vegetable crops for low-input, sustainable cropping systems (Navazio 2014, Mazourek 2014), as well as high-quality tomatoes targeted for direct marketing (Healy et al., 2015). Potential applications of this model should include consumer panels to evaluate whether selected phenotypes fulfill the expected sensory attributes of traditional heirloom varieties. Implementing regional PPB programs to develop 'Neo-heirloom' tomatoes can enhance productivity under local conditions and incorporate community-desired qualities. This premise could be extended in Hawai'i by following the objectives described in Casañas et al. (2017) and improving the traditional germplasm developed at The University of Hawai'i throughout the mid-twentieth century. To identify suitable traits for local production, future breeding programs must account for the unique seasonal variations and disease prevalence within and across each island’s microclimates. Moreover, given our research's differential relationship between yield and disease susceptibility, a comparative economic analysis of advanced genotypes with various disease resistances should supplement field experiments.

Heirlooms can exist in various material forms; whether jewelry, furniture, or a seed, the designation alludes to the continuation of culture and heritage (Heuss, 2012; Türe & Ger, 2016). While economic principles estimate an heirloom's monetary value, its intrinsic worth is inherent to the cultural history it represents. What defines an heirloom tomato? Whether or not the iconic label is what attracts customers, identifying its unmistakable sensory appeal will assist breeders in selecting phenotypes that satisfy market preferences. Through the ideas and analysis presented in this thesis, we hope to encourage a sustained interest in perpetuating the heirloom tomato in both conservation and future interpretation.

Supplementary Materials

Table 1. Experimental design details for the Waimānalo 2020 field trial.

Item	**Details**
Number of blocks	5
Number of treatments	23
Number of check treatments	7
Number of test treatments	16
Check treatments	*24-Karat, Black Krim, Farruco, Gelidonya, Pamela, Shining Star, Stealth*
Traits	Total Yield (kg/plant) Marketable Yield (kg/plant)

Table 2. The standard error for total and marketable yield (kg/plant) in Waimānalo 2020 field trial.

Comparison	***Marketable Yield (kg/plant)***	***Total Yield (kg/plant)***
A Test Treatment and a Control Treatment	0.66	0.71
Control Treatment Means	0.36	0.38
Two Test Treatments (Different Blocks)	0.85	0.91
Two Test Treatments (Same Block)	0.79	0.85

Table 3. Descriptive statistics for total and marketable yield (kg/plant) in the Waimānalo 2020 field trial.

Trait (kg/plant)	***Mean***	***Std.Error***	***Std.Deviation***	***Min***	***Max***	***Skewness***	***Kurtosis***	***CV***
Total Yield	2.1	0.29	1.38	0.32	5.21	1.15 *	3.28 ns	35.12
Marketable Yield	1.87	0.28	1.35	0.31	4.95	1.31 **	3.54 ns	37.32

ns $P > 0.05$; * $P \leq 0.05$; ** $P \leq 0.01$

Table 4. Experimental design details for the Honolulu 2021 field trial.

Item	**Details**
Number of blocks	5
Number of treatments	14
Number of check treatments	6
Number of test treatments	8
Check treatments	*Farruco, Marnouar, Old German, Pamela, Pink Smart, Quasimodo*
Traits	Total Yield (kg/plant) Marketable Yield (kg/plant)

Table 5. The standard error for total and marketable yield (kg/plant) in the Honolulu 2021 field trial.

Comparison	***Marketable Yield (kg/plant)***	***Total Yield (kg/plant)***
A Test Treatment and a Control Treatment	0.95	1.00
Control Treatment Means	0.51	0.53
Two Test Treatments (Different Blocks)	1.22	1.29
Two Test Treatments (Same Block)	1.13	1.19

Table 6. Descriptive statistics for total and marketable yield (kg/plant) in the Honolulu 2021 field trial.

Trait (kg/plant)	***Mean***	***Std.Error***	***Std.Deviation***	***Min***	***Max***	***Skewness***	***Kurtosis***	***CV***
Total Yield	3.69	0.54	2.01	1.45	9.26	1.49 **	5.19 *	20.20
Marketable Yield	2.99	0.48	1.78	0.87	7.88	1.48 **	5.04 *	22.47

ns $P > 0.05$; * $P \leq 0.05$; ** $P \leq 0.01$

Table 7.1 Descriptive statistics by market class predictions for the Hawai'i dataset. The Shapiro-Wilks test was used to estimate normality for each variable. For normally distributed variables, descriptive statistics are expressed as the mean and standard deviation, and significant differences were estimated from a one-way analysis of variance (ANOVA; P < 0.05). For non-normal variables, values are expressed as the median and first and third quartiles, and significant differences were estimated using the Kruskal-Wallis Test (P < 0.05).

	Prediction Groups		
Measurement (cm)	**Not Heirloom** ***n* = 252**	**Heirloom** ***n* = 93**	**P-value**
Perimeter	23.0 [21.2;25.7]	24.4 [22.4;27.0]	<0.001
Maximum Height	5.92 [5.38;6.38]	5.52 [5.03;5.96]	<0.001
Fruit Shape Index External I	0.80 [0.70;0.89]	0.66 [0.62;0.71]	<0.001
Distal Fruit Blockiness	0.81 (0.03)	0.83 (0.03)	<0.001
Fruit Shape Triangle	1.11 [1.07;1.14]	1.10 [1.05;1.13]	0.077
Rectangular	0.56 [0.54;0.57]	0.57 [0.55;0.58]	<0.001
Shoulder Height	0.09 [0.06;0.12]	0.15 [0.12;0.19]	<0.001
Proximal Angle Micro	203 [195;210]	197 [189;206]	0.001
Proximal Angle Macro	142 [124;155]	163 [89.3;176]	0.003
Proximal Indentation Area	0.28 [0.19;0.45]	0.58 [0.46;0.69]	<0.001
Distal Angle Micro	176 [92.6;180]	152 [88.3;181]	0.048
Distal Angle Macro	125 [113;137]	139 [132;148]	<0.001
Distal Indentation Area	0.00 [0.00;0.00]	0.00 [0.00;0.01]	<0.001
Distal End Protrusion	0.00 [0.00;0.01]	0.01 [0.00;0.03]	<0.001
Obovoid	0.00 [0.00;0.00]	0.00 [0.00;0.04]	0.001
Ovoid	0.16 [0.13;0.19]	0.14 [0.08;0.18]	0.004
V Asymmetry	0.07 [0.05;0.11]	0.10 [0.07;0.16]	<0.001
H. Asymmetry ob.	0.00 [0.00;0.00]	0.00 [0.00;0.04]	<0.001
H. Asymmetry ov.	0.15 [0.09;0.21]	0.11 [0.06;0.20]	0.047
Width Widest Position	0.45 [0.44;0.47]	0.46 [0.44;0.48]	0.558
Proximal Eccentricity	0.89 [0.89;0.89]	0.89 [0.89;0.89]	0.009
Distal Eccentricity	0.89 [0.89;0.89]	0.89 [0.88;0.89]	<0.001
Average Luminosity	136 [129;141]	129 [117;138]	<0.001
Average L Value	45.4 [41.5;57.3]	53.4 [42.6;60.3]	0.013
Average a Value	29.4 [24.7;31.7]	17.3 [10.1;24.5]	<0.001
Average b Value	29.3 [26.9;32.5]	32.5 [26.3;39.0]	<0.001
Average Chroma	41.5 [37.1;44.8]	39.0 [33.3;45.0]	0.039
Lobedness Degree	1.48 [1.10;2.13]	2.79 [2.09;3.80]	<0.001
Pericarp Area	0.44 [0.44;0.44]	0.44 [0.44;0.44]	0.901
Brix (%)	4.00 [3.66;4.33]	4.13 [3.83;4.50]	0.008
pH	4.36 [4.29;4.40]	4.27 [4.20;4.30]	<0.001
TTA (% CA)	0.47 [0.40;0.67]	0.68 [0.49;0.75]	<0.001
Class representation			
Commercial hybrid (CH)	124 (49.2%)	0 (0.00%)	
Heirloom hybrid (HH)	107 (42.5%)	32 (34.4%)	
Traditional heirloom (TH)	21 (8.33%)	61 (65.6%)	

Appendix A. Materials and Methods

Table 1. The Solanaceae Coordinated Agriculture Project (SolCAP) (a) vintage and (b) fresh market germplasm used to develop an heirloom market type classifier.

(a)

Vintage Germplasm (Oregon State University 2009-2010)	
Donor Number/Variety Name	**Line ID#**
1091-Chonto 21 (Mataverde 3-21-2)	SCT-0329
A-1770	SCT-0330
A-1771	SCT-0331
Abel	SCT-0332
Ailsa Craig	SCT-0325
Aker's West Virginia	SCT-0285
Amish Paste	SCT-0286
Beauty	SCT-0287
Black From Tula	SCT-0288
Brandywine (Sudduth/Quisenberry)	SCT-0290
Burbank	SCT-0291
Cherokee Purple	SCT-0292
Chih-mu-tao-se	SCT-0333
Costoluto Genovese	SCT-0293
Cotaxtla I	SCT-0334
Devon Surprise	SCT-0335
Favorite	SCT-0295
Globe	SCT-0296
Grushovka	SCT-0298
Heinz-1370	SCT-0336
Hong Kong	SCT-0337
Howard German	SCT-0299
Juane Flammee	SCT-0300
King Humbert	SCT-0301
Kiyosu No.2	SCT-0338
LA0410	SCT-0339
LYC1903	SCT-0302
Marglobe	SCT-0303
Marveille des Marches	SCT-0326
Moneymaker	SCT-0304
Opalka	SCT-0305
Orange Strawberry	SCT-0306
Oxheart	SCT-0307
Paragon	SCT-0308
Peron	SCT-0309
Peto 460	SCT-0340
PI124035	SCT-0341
PI124037	SCT-0342
PI128586	SCT-0344
PI128592	SCT-0345

PI129026	SCT-0346
PI129033	SCT-0347
PI129084	SCT-0348
PI159009	SCT-0352
PI196297	SCT-0353
PI270430	SCT-0355
PI272703	SCT-0356
Pomodoro Superselezione di Marmande	SCT-0357
Ponderosa	SCT-0327
Prospero	SCT-0358
Rinon PI118783	SCT-0360
Rinon PI118784	SCT-0360
Rinon PI98097	SCT-0359
Roma VF	SCT-0312
Rosao Monserrat	SCT-0361
Rumi Banjan	SCT-0362
Rutgers	SCT-0313
San Marzano	SCT-0314
Sao Paulo	SCT-0363
T1003	SCT-0317
T1693	SCT-0318
T1697	SCT-0319
Tomate del lugar	SCT-0365
Tres Cantos	SCT-0320
Turrialba	SCT-0366
White Queen	SCT-0322
Zhongza No.4	SCT-0369

(b)

Fresh Market Germplasm
(University of California Davis 2009-2010)

Donor Number/Variety Name	Line ID#
091109-3	SCT-0157
091119-2	SCT-0158
091120-2	SCT-0159
091120-7	SCT-0160
091135-1	SCT-0161
091144-2	SCT-0163
091166-3	SCT-0165
Campbell28	SCT-0172
‘Cherokee’	SCT-0173
Fla.678	SCT-0174
Fla.701	SCT-0175
Fla.7060	SCT-0176
Fla.7060	SCT-0237
Fla.7481	SCT-0178
Fla.7547	SCT-0179
Fla.7770	SCT-0181
Fla.7771	SCT-0182
Fla.7775	SCT-0183
Fla.7776	SCT-0184
Fla.7781	SCT-0185
Fla.7804	SCT-0186
Fla.7907B	SCT-0187
Fla.7946	SCT-0188
Fla.8000	SCT-0189
Fla.8044	SCT-0190
Fla.8059	SCT-0191
Fla.8109	SCT-0193
Fla.8111BH	SCT-0194
Fla.8124C	SCT-0195
Fla.8233	SCT-0196
Fla.8293	SCT-0198
Fla.8352	SCT-0200
Fla.8476	SCT-0201
Fla.8516	SCT-0202
Fla.8539	SCT-0203
Fla.8543	SCT-0204
Fla.8608	SCT-0207
Fla.8624	SCT-0208
Fla.8626	SCT-0209
Fla.8646	SCT-0211
Fla.8735	SCT-0213
Fla.8737	SCT-0214
Flora-Dade	SCT-0215
LA0797	SCT-0217
LA1996	SCT-0218
Legend	SCT-0224
Medford	SCT-0225

NC123S	SCT-0227
NC13G	SCT-0229
NC140	SCT-0230
NC161L-1 W(2007)	SCT-0231
NC1CS	SCT-0232
NC23E-2(93)	SCT-0233
NC2Y	SCT-0236
NC33EB-1	SCT-0237
NC47NC2	SCT-0238
NC50-7	SCT-0239
NC714-3B(2007)	SCT-0240
NC8276	SCT-0241
NC8288	SCT-0242
NCEBR-1	SCT-0246
NCEBR-3	SCT-0248
NCEBR-4	SCT-0249
NCEBR-8	SCT-0253
NCHS-1	SCT-0254
Ohio MR13	SCT-0256
Oregon Spring	SCT-0258
Oregon Star	SCT-0259
PI281553	SCT-0264
Piedmont	SCT-0268
Rio Grande	SCT-0269
Severianin	SCT-0270
Siletz	SCT-0271
Summit	SCT-0272
T-5	SCT-0273
T-9	SCT-0274
Tropic	SCT-0275
UC-MR20	SCT-0276
UC-N28	SCT-0277
UC-T338	SCT-0278
UC-TR44	SCT-0279
UC-TR51	SCT-0280
Willamette VF	SCT-0281

Figure 1. Sample preparations and assay protocol for Total Titratable Acidity (TTA), adapted from Healy et al. (2017) and Panthee et al. (2013).

Sample Preparation

Remove 50 ml samples from freezer and thaw at 4 °C.

Re-homogenate samples and bring to room temperature 20–22 °C.

Sample Dilution

Strain homogenate with cheese cloth to remove excess solids.

Perform 5-fold dilution

- 40 mL deionized water
- 10 mL strained homogenate

Total Titratable Acidity (Citric acid by volume)

Titrate with .1 N NaOH to 8.2 pH

% Citric acid (g/100 mL)= $(N * V_1 * \text{Eq wt.} * 100) / (V_2 * 1000)$

- N = Normality of NaOH (.1)
- V_1= Volume of NaOH added to reach titration point
- Eq wt.= Equivalent weight of citric acid (64 mg/mEq)
- V_2 = Original sample volume (50 mL)

Recorded as the mean % Citric acid from three technical replicates.

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