Received: 15 March 2022 | Revised: 27 June 2022 | Accepted: 11 July 2022

DOI: 10.1002/ppp3.10307

Plants People Planet PPP Open Access

BRIEF REPORT

What's in a name? The importance of identity in heirloom apple tree preservation

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Funding information

USDA National Institute of Food and Agriculture, Grant/Award Number: 1014919; National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: 1650115

Societal Impact Statement

Historic North American apple (*Malus domestica*) orchards that thrived in the late 19th and early 20th centuries, with cultivar compositions unlike today's orchards, are vanishing. There are several reasons for this loss: tree aging, cost of tree maintenance, and urbanization. Many groups have collected local knowledge regarding the history and horticulture of apples using both phenotypic and genotypic identification methods. Some of these groups have joined with scientists to form the collaborative "Historic Fruit Tree Working Group of North America" to facilitate the conservation of heirloom apple cultivars in North America through documentation, identification, collaboration, and education.

KEYWORDS

citizen science, conservation, cultivar, DNA fingerprinting, historical records, identification

1 | INTRODUCTION

Heirloom apple (*Malus domestica* Borkh.) cultivars, that is, varieties that were first named, replicated, and distributed over a century ago, exist across much of the North American landscape. These cultivars can be found in collections, commercial orchards, old homesteads, backyards, and on public lands (Bunker, 2019; Dunbar-Wallis et al., 2021; Volk et al., 2021b). The first North American apple trees were derived from either grafted clones of European cultivars or their seeds. These seeds represented new and unnamed genetic combinations likely chosen from desirable European cultivar mothers. Once matured from seedlings into bearing trees, some were selected for their exhibited desirable attributes, such as bountiful yield, long storage, appealing color, and enticing aroma. Commercial growers, breeders, and enthusiasts named such potentially valuable trees and grafted them onto rootstocks to generate multiple trees with the same set of characteristics. The earliest named cultivars in British North America were these named selections, and over time, nurseries, farmers, and others began to share or sell these cultivars to such an extent that they spread widely. In this way, a genetically unique single tree with a desirable combination of attributes could be transformed into a cultivar of dozens to thousands of trees for farmers and consumers in many regions to appreciate. Thousands of cultivars—named and now considered heirlooms—were created and subsequently documented in North America (Bussey, 2016; Volk & Henk, 2016), including those described in nursery catalogs that have been made available through the National Agriculture Library (USDA, 2022a). Dozens of cultivars were typically grown in each apple orchard until the early 1900s, and these trees provided long-term stability to farms and homesteads as sources of human and animal food, juice for hard cider and vinegar, and income from sales to local communities (Dolan, 2009).

Remarkably, many apple trees and orchards planted by previous generations are still alive today. Apple trees have an average lifespan of 80–140 years, and many heirloom trees are nearing the end of their lifespans. Most extant heirloom trees are distinct from those grown in modern-day orchards. These heirloom trees are often larger, require less maintenance, and may have fruit characteristics different from those of modern cultivars. Together, these trees represent a secondary center of diversity for the crop beyond its Eurasian origin and add to the agrobiodiversity of the continent (Diamond, 2010; Routson et al., 2009; Volk et al., 2015). Community organizations, land managers, and conservation groups have recognized the value of surviving heirloom apple trees and have undertaken coordinated efforts to locate, identify, and preserve aging trees before they are lost. But as each old tree is found, the cultivar it represents is often unknown. While many trees are cultivars that are already well preserved, others might be the last survivor, with unique and valuable alleles or allelic combinations. Accurate cultivar identification is critical for the success of apple conservation efforts.

2 | APPLE CULTIVAR IDENTIFICATION

Until recently, identification of specific apple cultivars required comparison of vegetative and fruit traits among possibly hundreds of trees grown in a region. Phenotypic identification efforts are limited by the knowledge of the identifiers, who are dependent upon local histories, oral accounts, nursery catalogs, and personal familiarity with a wide range of cultivars. The USDA commissioned a set of watercolor paintings between 1886 and 1942, many of which have been scanned and made available by the National Agriculture Library (USDA, 2022b). The paintings were originally created to document the vast number of cultivars and are still helpful for identifying heirloom trees today. Additional key resources are the National Agriculture Library's digitized nursery catalog collection (USDA, 2022a) and the “American Fruit Book” (Cole, 1849), an early guide for orchardists and growers that contains descriptions and generalized fruit shape outline drawings of more than 250 cultivars and synonyms. Identification books such as “The Apples of New York” (Beach, 1905) carefully defined and described the morphological variation among apple fruit in general and described and illustrated typical features of many cultivars. A more recent landmark book describing apple cultivars is the seven-volume “The Illustrated History of Apples in the United States and Canada” (Bussey, 2016) that uses USDA watercolors and descriptions of each cultivar's characteristics up to the year 2000–16,350 of them. Online resources such as applename.com and fruitid.com can also be used to identify cultivars; however, the number of cultivars contained in those resources is limited. As with all fruit crops, some apple traits vary with the environmental conditions under which they are grown, thereby complicating the visual identification process.

Regional experts have developed detailed and time-consuming methods to phenotypically identify common local cultivars. The first step is determining if a tree is a cultivar that arose from grafting or if it is a seedling tree that arose from its own seed and thus unlikely to be named. Ten fruit from each tree are typically used in the identification approach described in Method S1. Phenotypic apple cultivar identification is difficult, however, because (1) some traits are highly variable based on growth location, tree age, rootstock, and so forth; (2) many cultivars are phenotypically similar; (3) there are many cultivar synonyms (i.e., same cultivar and different names) that were not fully realized until genotypic data became available; (4) information is sparse for some heirloom cultivars; (5) each identification is onerous; and (6) few people have acquired the necessary expertise.

DNA fingerprinting technologies have revolutionized the apple cultivar identification process by using genotypic data instead of phenotypic data to determine the identity of trees of interest. The success of genotyping for identification (Method S1b) is dependent upon having reference DNA fingerprints available for large collections of verified-identity cultivars, such as the reference specimens available in genebanks (including the USDA National Plant Germplasm System Apple Collection in Geneva, NY), heirloom orchards, and breeding collections (Gutierrez et al., 2020). Small sets of microsatellite markers were used to characterize apple cultivar collections (Gross et al., 2012; Guilford et al., 1997), which provided genotypic datasets that then served as reference panels for identifying unknown cultivars (Venison et al., 2022; Volk et al., 2021a, 2021b), cultivar synonyms, and mislabeled accessions (e.g., Evans et al., 2011; Gross et al., 2012). These genotypic datasets were useful but limited because of difficulties such as comparing datasets among laboratories (Evans et al., 2011; Gross et al., 2012; Venison et al., 2022). Despite limitations, these efforts resulted in establishing the cultivar identities of hundreds of heirloom trees in the North American landscape (Routson et al., 2009; Volk et al., 2021a, 2021b; Volk & Henk, 2016).

Recently, apple collections and breeding materials have been genotyped using the new technology of single nucleotide polymorphism (SNP) arrays. Apple SNP arrays (Bianco et al., 2014, 2016; Chagné et al., 2012) have enabled robust comparisons of materials among collections internationally and thereby facilitated development of large, reliable reference panels. SNP arrays efficiently provide much higher genotyping resolution than microsatellite marker sets by dramatically increasing the number of chromosomal positions assayed, enabling pedigree reconstruction (Howard et al., 2017, 2021) that increasingly ties apple cultivars together into a vast relationship network. Consideration of a tree's pedigree information in the context of historical information about a cultivar can be useful in ensuring correct identification (Howard et al., 2017; Peace et al., 2021). Despite the power of this new technique, most sports (spontaneous mutations with distinct phenotypes) are still not genotypically distinguishable (Kumar et al., 2022).

Genotyping of trees of interest in the US using SNP arrays has been used to assign accurate heirloom cultivar names for old trees, informing collection managers and heirloom apple organizations and individuals. Washington State University's (WSU's) Department of Horticulture is providing definitive answers to cultivar name mysteries for more trees and for a wider range of people than ever before (Table 1) by offering SNP array-based investigation of cultivar identity and parentage to the U.S. public on a cost-recovery basis via the MyFruitTree project (Peace & Johnson, 2022). This venture mobilizes the expertise of apple geneticists, collection managers, growers, and historians to develop a large reference panel of heirloom and modern U.S. cultivars. More than 500 publicly submitted samples in the previous 2 years have been merged with international research datasets that include thousands of cultivars, selections, and seedlings. For the hundreds of samples submitted with cultivar names based on oral history or phenotypic identification, a sixth were confirmed (with the same names or their known synonyms already in the dataset), half were new additions to the dataset, and a third were misnamed and matched instead to a different cultivar (Peace, 2021). For example, a tree from Maine that was initially thought to be “Briggs Auburn” was genotypically identified as “Northwest Greening.” The original phenotypic identification was based on available printed books and catalogs, and it was assumed that “Northwest Greening” was a cultivar too recent for consideration. In an example of historical synonyms, oral histories identify many trees as “Gano” in SW Colorado that are genotypically “Ben Davis”—it is suspected that growers in the region had a general bias against using the name “Ben Davis” when the trees were originally planted. In some cases of confirmed identity, the tree represented a cultivar that was historically documented but thought extinct. Careful historic research, comparisons with prior documentation, a unique DNA profile, and an appropriate pedigree position provide confidence that an heirloom cultivar has been rediscovered, such as the case with “Colorado Orange” (Schuenemeyer & Schuenemeyer, 2022) and “Sary Sinap” (NPR, 2021). For the hundreds of trees with unknown identity tested by WSU's MyFruitTree project, cultivar names have been determined for approximately half of them. For the other half of the tested trees, while some were already known by the submitter to be seedlings, many could be heirloom cultivars with their true name still unknown. Results obtained from these efforts are helping to broaden scientific knowledge about differences and relatedness among cultivars.

3 | AN INTEGRATED APPROACH

A shared interest in heirloom apple cultivar identification has brought together apple enthusiasts, ranging from scientists to historians to conservation groups and members of the public. This community (including all authors of this paper) has formed the Historic Fruit Tree Working Group of North America (Video 1). The Working Group's mission is to facilitate the conservation of fruit tree cultivars in North America through documentation, identification, collaboration, and education via the following activities.

1. Document the historical importance of fruit tree cultivars.
2. Verify cultivar identities using a standardized naming process including DNA profiling.
3. Record conservation efforts and commercial availability of fruit tree cultivars by developing collaborative, interoperable information systems.
4. Create and maintain geographical cataloging tools for fruit tree documentation.
5. Provide networking opportunities for the fruit tree conservation community, including developing a public web interface that facilitates education and collaboration.

Recently, the Working Group developed and released mapping tools to georeference and document named and yet-to-be-named fruit trees of interest and historic orchards. The mapping platforms, namely, the Fruit RegisTREE and Orchard RegisTREE, are publicly available (Schuenemeyer et al., 2021; Uhlmann et al., 2021) and have facilitated communication and fostered relationships among heirloom fruit tree enthusiasts. The results of this first effort in building an online community platform as well as ongoing mission-focused projects are expected to inform and educate fruit growers, breeders, students, and community members about the importance, characteristics, histories, and availability of heirloom cultivars. One potential drawback of this mapping method is that trees on private property could be reported without the property owner's permission. Further, some may use the map as a guide to trees for fruit gleaning purposes without first seeking permission from owners. Efforts have been made throughout the RegisTREE to encourage users to have all appropriate permissions prior to mapping and visiting sites.

To determine the cultivar name of any tree of interest—particularly once the tree has been added to the Fruit RegisTREE—the Working Group has developed an integrated two-stage approach (Figure S1). The first stage is to establish if the tree is identical to a known cultivar. Phenotyping (such as comparing against pictures and descriptors of a region's most common cultivars or using a diagnostic key) or genotyping (especially with a relatively quick and cheap method such as small sets of microsatellite markers) is conducted to efficiently identify the cultivar name wherever possible. For trees that cannot be readily identified using basic phenotyping or genotyping or to confirm the identity with greater confidence, higher resolution genotyping with SNP arrays is conducted via MyFruitTree. The second stage is to assign a cultivar

TABLE 1 Example outcomes from SNP (single nucleotide polymorphism) array-based genotyping of U.S. apple trees

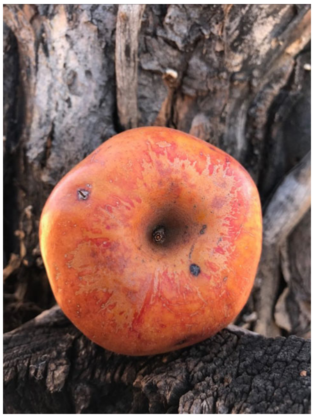
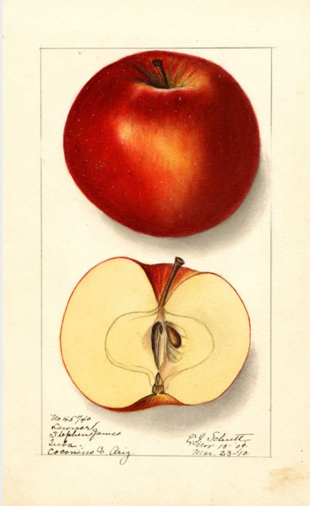
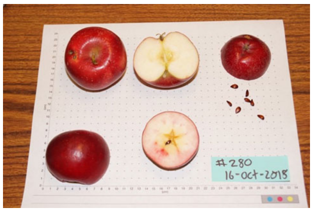
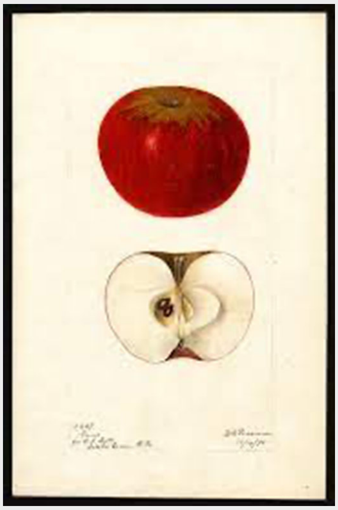
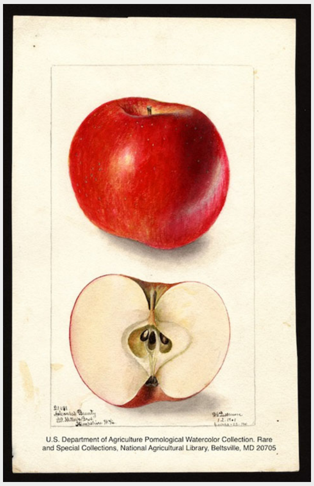
Possible outcome	Example	Image
1. Adds a cultivar to the dataset	The cultivar "Colorado Orange" found by Montezuma Orchard Restoration Project (MORP) and carefully compared to U.S. Department of Agriculture (USDA) watercolors, historical written descriptions, and wax apple displays at Colorado State University, helped to phenotypically identify the fruit. DNA fingerprinting determined this tree does not match any other in the large international dataset. Therefore, the tree is likely to be "Colorado Orange" and represents a new addition to the dataset. *Photo credit: Montezuma Orchard Restoration Project*. See also the "Sary Sinap" that was rediscovered by the Lost Apple Tree Project (NPR, 2021).	
2. Adds a cultivar to the dataset and fills a pedigree gap	The "Lawver" cultivar was at first not in the dataset but was the predicted parent of three individuals in the dataset (and the predicted offspring of "Yellow Bellflower"). Collaborator Nicholas Howard of the University of Minnesota made this deduction. One of these offspring had breeding records indicating "Lawver" x "McIntosh" as parents. As the DNA profile for "McIntosh" was already in the dataset, the other parent was assumed to be "Lawver," represented by half the DNA profile of that offspring. The samples from two unnamed trees submitted to MyFruitTree had identical DNA profiles with each other and fit as the missing individual in the pedigree. Photographic images of the fruit provided with the submitted samples matched well with "Lawver" in the USDA Watercolor collection. Further evidence came from two more recent sample submissions from MORP, both of which were noted as being "poss. Lawver" based on phenotype. *Photo credit: U.S. Department of Agriculture Pomological Watercolor Collection. Rare and Special Collections, National Agricultural Library, Beltsville, MD 20705*	
3. Confirmed cultivar name	The "Delicious" cultivar was widely planted in Boulder County, Colorado, USA, in the early 1900s. Several properties on remnant orchard sites have apple trees bearing fruit with the distinctive five "lobes" near the basin. One particular former orchard had planting records that included "Delicious." DNA fingerprinting confirmed this cultivar identity. *Photo credit: Boulder Apple Tree Project*.	
4. Identifies historical synonyms (regional names)	The cultivar "Ben Davis" was widely planted in the early 20th century but anecdotally fell out of favor due to a preference for other cultivars. Leaf samples from MORP trees noted as "Ben Davis poss. Gano" were determined by DNA fingerprinting to be "Ben Davis." *Photo credit: U.S. Department of Agriculture Pomological Watercolor Collection. Rare and Special Collections, National Agricultural Library, Beltsville, MD 20705*	

TABLE 1 (Continued)

Possible outcome	Example	Image
5. Refutation that an old tree is a particular old cultivar	A tree that was thought to be "Briggs Auburn" in Maine, USA, based on available literature at the time (more information in Ch. 10 of Apples and the Art of Detection; Bunker, 2019) is actually a "Northwest Greening." *Photo credit: John Bunker*.	
6. Corrects cultivar names in the dataset	A tree each of "Red Gem" and "Granny Smith Red" (known synonyms, maintained in the Grove collection in Tasmania, Australia) were DNA-fingerprinted and at first added a new DNA profile to the dataset. This cultivar has its own recent origin story in Australia. Then an old tree growing at Steptoe Butte, Washington, USA, identified as "Arkansas Beauty" was DNA-fingerprinted, and was identical to those "Australian" trees. "Arkansas Beauty" originated in the late 1800s, probably in Arkansas. So it appears that "Red Gem"/"Granny Smith Red" in Australia arose as a mislabeled or forgotten import of the U.S. cultivar "Arkansas Beauty." A parent is "Jonathan." *Photo credit: U.S. Department of Agriculture Pomological Watercolor Collection. Rare and Special Collections, National Agricultural Library, Beltsville, MD 20705*	
7. Cultivar name determined	A tree from Boulder County Open Space, Colorado, USA, that grows along well-traveled hiking trails and was not part of a known orchard planting but was very near to known homesteading sites had a DNA profile matching "Winter Banana." *Photo credit: Boulder Apple Tree Project*.	
8. Unknown cultivar name but further research could uncover the identity	This tree is known as BATP (Boulder Apple Tree Project) 498 does not match with any known cultivar but has DNA fingerprint matches across Colorado, Montana, and Wyoming. Therefore, it has been cloned and grown in multiple orchards and is likely a cultivar that was once commercially available. BATP 498 was determined to have "Grimes Golden" and "Wealthy" as parents, two popular cultivars in the region a century ago. *Photo credit: Boulder Apple Tree Project*.	

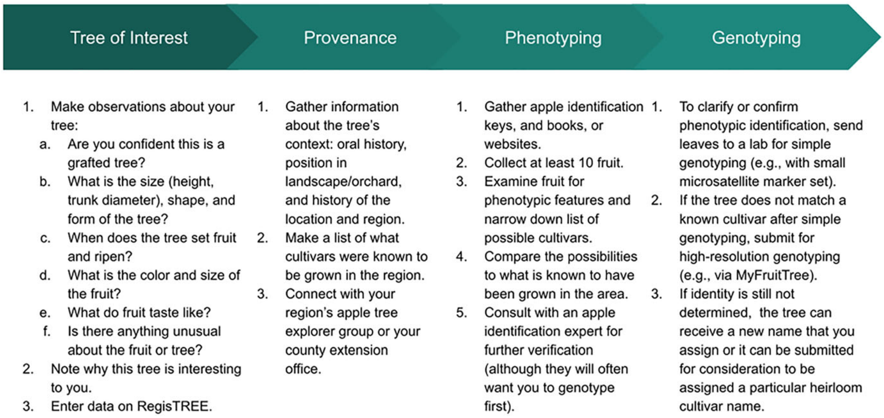
Note: Collection managers and other fruit enthusiasts have submitted leaf samples for hundreds of their U.S. apple trees of interest to MyFruitTree (Peace & Johnson, 2022) over the last several years. Some samples arrive with cultivar names tentatively attached—many have provided new DNA profiles additions to the international dataset, although confirming their name often requires further consideration of historical records, phenotypic features, and pedigree revelations. Others have had their attached name confirmed. Still, others have been determined to not be the cultivar they were thought to be or revealed an identity mistake in the dataset. Samples submitted without a cultivar name, unless they were a known seedling, often matched to known cultivars, while others are suspected to represent heirloom cultivars—with historical research needed to uncover their identity.

VIDEO 1 Apple exploration groups and individuals have joined with scientists to form the collaborative "Historic Fruit Tree Working Group of North America" to facilitate the conservation of heirloom apple cultivars in North America through documentation, identification, collaboration, and education. This animated map shows the location of the current Working Group participants, the mission of the group, and introduces some of the locations of historic trees as found on the RegisTREE website.
Video content can be viewed at https://onlinelibrary.wiley.com/doi/10.1002/ppp3.10307

name to trees unidentified in the first stage. If a tree is suspected to be an heirloom cultivar that has not been identified before, evidence is gathered by the proposer and evaluated by an expert panel for the degree of alignment between the tree of interest and the heirloom cultivar considering provenance, phenotype, and genotype as described in Figure 1.

4 | A CALL FOR COMMUNITY ACTION

Community access to genotyping, shared mapping resources, historical information, and phenotyping expertise, as well as reliable information for each cultivar including parentage and origins, synonyms, and observed and expected performance, has made it possible for a wide range of engaged community members to become involved in apple conservation activities. Figure 1 summarizes how interested people can take action. Members of the public can become citizen scientists in this venture by adding data, information, and knowledge including (1) more apple tree and orchard locations through the Fruit RegisTREE; (2) verification of cultivar identity of heirloom trees by phenotypic and genotypic assessments (through MyFruitTREE); (3) observations on cultivar performance in certain locations and years (especially standardized phenotyping for highly heritable traits); (4) additional discoveries of old trees representing lost cultivars; and (5) further exploration and synthesis of historical records. Within academia, course-based undergraduate research opportunities provide key avenues for heirloom apple conservation. For example, students and volunteers in the Boulder Apple Tree Project locate and map trees, collect and research oral histories, and compile morphological



Tree of Interest	Provenance	Phenotyping	Genotyping
1. Make observations about your tree: a. Are you confident this is a grafted tree? b. What is the size (height, trunk diameter), shape, and form of the tree? c. When does the tree set fruit and ripen? d. What is the color and size of the fruit? e. What do fruit taste like? f. Is there anything unusual about the fruit or tree? 2. Note why this tree is interesting to you. 3. Enter data on RegisTREE.	1. Gather information about the tree's context: oral history, position in landscape/orchard, and history of the location and region. 2. Make a list of what cultivars were known to be grown in the region. 3. Connect with your region's apple tree explorer group or your county extension office.	1. Gather apple identification keys, and books, or websites. 2. Collect at least 10 fruit. 3. Examine fruit for phenotypic features and narrow down list of possible cultivars. 4. Compare the possibilities to what is known to have been grown in the area. 5. Consult with an apple identification expert for further verification (although they will often want you to genotype first).	1. To clarify or confirm phenotypic identification, send leaves to a lab for simple genotyping (e.g., with small microsatellite marker set). 2. If the tree does not match a known cultivar after simple genotyping, submit for high-resolution genotyping (e.g., via MyFruitTree). 3. If identity is still not determined, the tree can receive a new name that you assign or it can be submitted for consideration to be assigned a particular heirloom cultivar name.

FIGURE 1 Documenting and identifying your apple tree via the integrated approach proposed by the Historic Fruit Tree Working Group of North America
Community members and citizen scientists are welcome to join our efforts in identifying, cataloging, and preserving historic apple cultivars. Once you have worked through the general features of your tree of interest and recorded it in the RegisTREE, if you are curious about its cultivar identity, you can gather clues from its provenance to line up likely suspects. Next, with at least 10 fruits on hand, you can conduct phenotyping to narrow down the possibilities and even find a match. Instead, or in addition to phenotyping, you can submit your leaf samples to a genotyping laboratory for a fee.

tree data (Dunbar-Wallis et al., 2021). At the College of the Atlantic, faculty and students have mapped and documented hundreds of heirloom trees and seedlings. Online tools in development at WSU are expected to enable anyone to explore and even deduce pedigree relationships among apple cultivars and inheritance paths of attributes of interest. A planned one-stop Apple Cultivar Database will enable the interested public to learn about local cultivars and where trees can be obtained. Growers will be able to learn what performance to expect from each cultivar. Cooperation among apple enthusiasts—including seed and scion swapping groups, hobbyist organizations, citizen scientists, conservation groups, and public institution educators and research scientists—has created educational opportunities and expanded knowledge about heirloom apple cultivars in the North American landscape.

ACKNOWLEDGEMENTS

USDA is an equal opportunity employer and provider. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 1650115 and by the USDA National Institute of Food and Agriculture Hatch project 1014919, Crop Improvement and Sustainable Production Systems (WSU reference 00011). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation or USDA.

CONFLICT OF INTEREST

The authors have no conflict of interest to report.

AUTHOR CONTRIBUTIONS

ADW, AMJ, CPP, GMV, and JB contributed to drafting this manuscript. ADW, AMJ, CPP, DC, and JB prepared the figures and supporting information. ADW, AMJ, AS, CPP, DB, GMV, LS, LP, RU, and TL-S edited the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Dunbar-Wallis, A., Volk, G. M., Johnson, A. M., Schuenemeyer, A., Bunker, J., Castro, D., Little-Siebold, T., Pendergast, L., Uhlmann, R., Sieger, L., Benscoter, D., & Peace, C. P. (2023). What's in a name? The importance of identity in heirloom apple tree preservation. *Plants*, *People*, *Planet*, *5*(1), 39–46. https://doi.org/10.1002/ppp3.10307