Extended Pedigrees of Apple Cultivars from the University of Minnesota Breeding Program Elucidated Using SNP Array Markers

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Abstract. Apple (*Malus ×domestica* Borkh.) breeding at the University of Minnesota (UMN) has been ongoing continuously since 1908 when staff originally planted thousands of seedlings from open-pollinated (OP) seeds collected from regional orchards. The first cultivar from the program, ‘Minnehaha’, was introduced in 1920 and several others from these OP seeds followed over the next 3 decades. Controlled crosses were initiated in 1916, and until the time of this publication, 28 cultivars have been introduced. Historical records of parentage, as recorded by staff in notebooks and in 20th-century publications, have been used to inform breeding decisions but might be incorrect as indicated by earlier explorations of parentage using simple sequence repeat (SSR) markers. Our objective was to elucidate parentage and extended pedigrees of all available cultivars introduced from the UMN apple breeding program using evaluations of Mendelian errors and shared haplotype length information based on data from single nucleotide polymorphism (SNP) arrays. Sixteen of the 21 cultivars introduced before ‘Honeycrisp’ (1991) had incorrect or incomplete pedigrees that are now at least partially elucidated. These include the two most important regional cultivars in the 20th century: ‘Haralson’ (parents: ‘Malinda’ and ‘Wealthy’) and ‘Fireside’ (parents: ‘Wealthy’ and ‘Northwest Greening’). ‘Wealthy’, a widely grown cultivar in the United States in the late 19th and early 20th centuries, was a frequent parent of older UMN cultivars. ‘Malinda’ was a less frequent parent than indicated by breeding records. ‘Duchess of Oldenburg’ (synonym ‘Borowitzky’) was revealed as an ancestor of overwhelming importance in the UMN breeding program. It was an ancestor of 27 of the 28 UMN cultivars, including as a parent of two cultivars, and a grandparent of 15 cultivars, including ‘Honeycrisp’.

Apple (*Malus ×domestica* Borkh.) breeding at the UMN began in 1878 as an effort to develop cultivars of high fruit quality that could “meet the extremes of [Minnesota’s] mid-continental climate” (Alderman et al., 1957). For apple production, Minnesota’s climate was considered “favorable, except for a short time during exceedingly severe winters” (Green, 1903). The terms “hardiness” or “winterhardiness” were often used by horticulturists of the Midwest and Great Plains region of the United States and Canada in the late 19th and early 20th century. For example, Saunders (1911) described an “entirely hardy” cultivar as having “never been injured by winter,” growing “from terminal buds on the branches every season,” and “fruiting abundantly for many years.” Cultivars were often compared based on relative performance for these criteria. Green (1903), for example, provides lists indicating relative regional adaptation of cultivars of his time by listing them in groups from “first degree” and “second degree of hardiness” to cultivars that were “valuable in some locations.”

Peter Gideon, developer of the ‘Wealthy’ apple, led a participatory UMN breeding program from 1878 until 1889 by distributing about 10,000 seedlings to Minnesota horticulturists (Green, 1903). By the turn of the century, Russian cultivars introduced to Minnesota circa 1880, along with some seedlings of local origin, including ‘Wealthy’, were considered the best available varieties by Samuel Green, the first UMN professor of horticulture (Green, 1903). In 1907, the Minnesota Legislature funded the purchase of land to establish a Fruit Breeding Farm near Excelsior, MN, under the management of the Minnesota Agricultural Experiment Station and the UMN (Alderman, 1944). The staff of the program rapidly planted many thousands of seedlings at the new facility. Most were from open-pollinated (OP) seeds collected from regional orchards (Dorsey, 1919). The first cultivar from the program, ‘Minnehaha’, was introduced in 1920, and several others from these initial OP seeds followed over the next 3 decades (Luby, 1991). Controlled crosses were initiated by 1916 (Horticultural Research Center, 1922). To date, 28 cultivars

have been introduced by the program (Table 1). These cultivars have been widely planted regionally (Gross et al., 2018) and ‘Honeycrisp’, ‘Minneiska’, and ‘MN55’ have been commercialized internationally.

Parentage information is commonly presented in the nursery trade for growers to consider in cultivar choice for new plantings. Parentage and extended pedigree information can be useful in breeding programs to identify related individuals that may share phenotypes or breeding potential due to shared genomic content that is identical by descent from common ancestors. In the past, breeders had to rely on pedigrees, cultivar descriptions, photos, and colored lithographs recorded by reputable, scrupulous, and knowledgeable colleagues and preceding breeders to confirm identities and pedigrees (for examples, see Bussey, 2016). With the availability of relatively inexpensive and abundant genome-wide DNA markers in the past 2 decades, the extended pedigrees of cultivars can be reconstructed with great certainty (Howard et al., 2017), especially when relatives are extant to confirm phasing of markers (Howard et al., 2021a).

Parentages of UMN cultivars were recorded in notebooks (Farrell et al., 2019) and summarized in publications throughout the 20th century (Alderman, 1926; Alderman et al., 1957; Luby, 1991). As in any breeding program, however, procedures for crossing, seed and seedling handling, as well as clonal propagation, can introduce opportunities for errors in recorded parentage. As polymerase chain reaction techniques for inexpensive, rapid, and accurate DNA fingerprinting became available in the 1990s, program staff and collaborators sought to confirm parentage or identify previously unknown parentage of introduced cultivars and unnamed selections in the program (Cabe et al., 2005). More recently, the development and use of single nucleotide polymorphism (SNP) marker arrays for apple (Bianco et al., 2014, 2016; Chagné et al., 2012) have enabled greater depth of pedigree reconstruction efforts (e.g., Muranty et al., 2020; Skytte af Sætra et al., 2020; van de Weg et al., 2018). Initial explorations of the parentage of University of Minnesota cultivars using simple sequence repeat (SSR) markers identified several instances where genotypes were inconsistent with recorded parents (Cabe et al., 2005). A later follow-up study using SNP haplotypes allowed identification of a parent of the cultivar Honeycrisp that is no longer extant (Howard et al., 2017).

In addition to confirming or correcting historical records, cultivar parentage determined by examining DNA markers can also provide insights into the germplasm foundations of a breeding program and the shared ancestry of cultivars. Apple trees are long-lived perennial plants with a gametophytic self-incompatibility system (Ramirez and Davenport, 2013). Cultivars are clonally propagated, usually as compound plants grafted on rootstocks. These characteristics have enabled long-term preservation of individuals in germplasm collections and breeding programs so that important ancestral cultivars may be used repeatedly

in breeding over decades or even centuries. The availability of plentiful, inexpensive SNP markers for older cultivars (e.g., Muranty et al., 2020) and new analytical tools (Howard et al., 2021a, 2021b) enable determination of detailed, extended pedigrees that were previously unknown (Howard et al., 2021a). Extended pedigrees can inform breeders' future crossing decisions by providing knowledge of inbreeding and by identifying parents that are putative carriers of desirable or undesirable alleles based on their shared ancestry (Howard et al., 2018b). The usefulness of pedigree reconstruction in correcting breeding records and for informing breeding decisions is the impetus for the current study. Our objective in this report was to determine parentage and extended pedigrees of available cultivars introduced from the UMN apple breeding program using SNP array data and newly available methods for the elucidation of extended pedigree relationships.

Materials and Methods

Plant material. All 28 UMN cultivars, their recorded parents, and ancestral selections and cultivars were genotyped for pedigree reconstruction (Supplemental Table 1). The individuals used in the study were cataloged by MUNQ codes (for *Malus* UNiQue genotype codes;

Denancé et al., 2020), which were defined to facilitate international comparison of apple genetic resources as a development from the FBUNQ code described by Urrestarazu et al. (2016) based on SSR marker data. Individuals with the same MUNQ code are genotypic duplicates. These accessions are part of a large MUNQ code dataset (Denancé et al., 2020). Individuals that lacked SSR data and thus typical MUNQ attribution were given provisional MUNQ codes, typically derived from accession id numbers. Leaves from UMN cultivars were collected from orchards at the UMN Horticultural Research Center near Chaska, MN, and several other locations. Because many cultivar releases were reported as resulting from OP or unknown parentage, an effort was made to sample cultivars known to be historically grown in Minnesota (Green, 1903) and extant cultivars listed in early UMN pollination records extending back to 1916 (Horticultural Research Center, 1922, 1927, 1931, 1935, 1941, 1949, 1951, 1955). Additionally, SNP array data for more than 5000 cultivars and germplasm accessions included in a concurrent large-scale collaborative apple pedigree reconstruction project (Howard et al., 2018a) and for more than 1400 cultivars included in a previous pedigree reconstruction study (Muranty et al., 2020) were also included for the pedigree reconstruction of the UMN cultivars.

Genetic data. Cultivars and breeding selections were genotyped either on the Illumina Infinium 20K apple SNP array (Bianco et al., 2014) with DNA extracted as described by Clark et al. (2014), or on the Axiom Affymetrix apple 480K SNP array (Bianco et al., 2016) as described by Muranty et al. (2020). SNP call data from both arrays were integrated in Howard et al. (2021b). A combined dataset was processed and curated as described in Vanderzande et al. (2019) to address Mendelian errors, creating a highly accurate dataset suitable for detailed pedigree reconstruction. The genetic map used was an edited form of the iGLmap (Di Pierro et al., 2016) described in Howard et al. (2021b) and included 10,295 SNPs.

Pedigree reconstruction. Parent–offspring and parent–parent–offspring relationships were identified following the methods of Vanderzande et al. (2019), which relied on the identification of Mendelian inconsistent errors. In short, SNP calls between individuals and their prospective parent(s) were checked to be consistent with Mendelian inheritance. These relationships were considered true if they lacked Mendelian inconsistent errors across >99.9% of SNPs. The possibility of <0.1% errors was accepted because there are occasionally rare, undiagnosed technical issues or rare biological peculiarities (small deletions, duplications, new mutations, etc.) that can cause Mendelian errors that are not easily resolved or explainable in cluster plot data. Typically, there were no unexplainable Mendelian errors between individuals and their parent(s) following the SNP data curation methods used. Additionally, the possibilities of Mendelian errors arising from eu/aneuploidy were checked using methods described in Vanderzande et al. (2019). Other

relationship types, particularly grandparent–grandchild relationships, were identified using methods described in Howard et al. (2021a). These methods made use of the interpretation of summed potential lengths of shared haplotype information generated using HapShared, a custom Python script. Phased SNP genotypic data used in these methods were generated using FlexQTL (Bink et al., 2014; Howard et al., 2021a). Individual grandparent–grandchild relationships were considered confirmed when they followed the type of logic described in the grandparent–grandchild relationship case study included in Howard et al. (2021a). In short, the following evidence was required for a grandparent–grandchild relationship to be considered confirmed: 1) extended haplotypes in a likely grandparent needed to be shared with about the expected 50% of the homologs of the likely grandchild; 2) if phased haplotype data for the prospective grandparent and its prospective grandchild were available, some evidence of extended haplotypes in the grandchild being composed of recombinant haplotypes from the grandparent was needed; 3) haplotypes from the prospective grandparent had to cover roughly 50% of the ends of the homologs of the prospective grandchild; and 4) a grandparent needed to be older than its grandchild (when reputable provenance information was available) such that they could reasonably have been in the lineage of a UMN cultivar based on introduction date (Table 1). Pairs of grandparents constituting the pedigree of an ungenotyped parent of an individual were considered confirmed when there were no Mendelian inconsistent errors present in such a matchup as also described in Howard et al. (2021a).

Results and Discussion

Pedigree reconstruction of UMN cultivars.

Partial or complete pedigrees could be reconstructed for each UMN cultivar based on SNP markers. The parentages as recorded by staff and as either confirmed (plain typeface) or identified in this study (bold typeface) are presented in Table 1. Available markers could not distinguish whether a parent served as female or male parent. For some cultivars, grandparents through an unknown or ungenotyped parent could be identified but not the actual parent itself.

Sixteen of the 21 cultivars introduced in the 20th century before ‘Honeycrisp’ had incorrect or incomplete recorded parentages that we could at least partially elucidate. In the early decades of the program, breeders selected prolifically among seedlings having OP origins to quickly identify adapted types (Dorsey, 1919). More than 1000 selections from OP seedlings were made from the 1910s through 1930s. Of the 14 cultivars introduced from these early selections, records indicated that five had unknown parentages and nine were from OP of specified maternal parents. We were able to identify at least one of the parents for each of the five cultivars with recorded unknown parentage. Of the nine cultivars with OP origin, the recorded seed parents of only three were

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Table 1. Cultivars introduced by the University of Minnesota apple breeding program with their parentages as recorded in breeding records and parentages as indicated by SNP haplotype analysis. Parents or grandparents in bold typeface in the Actual parent columns were identified using SNP array markers in this study.

Cultivar	Associated trademarks	Selection number	Yr introduced	Recorded cross	Actual parent 1	Actual parent 2
Haralson		90	1922	Malinda open-pollinated (OP) ^z	Malinda	Wealthy
Wedge		207	1921	Ben Davis OP ^z	(Malinda × Duchess of Oldenburg)	Northwest Greening
Folwell		237	1921	Malinda seedling OP ^z	Duchess of Oldenburg	(Alexander × Golden Russet)
Chestnut		240	1949	Malinda OP ^z	Wealthy	(Keswick Codlin × ?)
Minnehaha		300	1920	Malinda OP ^z	Wealthy	(Ben Davis × Fameuse)
Victory		396	1943	McIntosh OP ^z	McIntosh	Wealthy
Beacon		423	1936	Malinda OP ^z	(Malinda × Duchess of Oldenburg)	(Malinda × Tetofsky)
Frostbite		447	2008	Unknown	(Duchess of Oldenburg × Utter's Large Red)	—
Redwell		638	1946	Scott Winter OP ^z	Wealthy	(Alexander × ?)
Minjon		700	1942	Unknown ^z	Malinda	Wealthy
Oriole		714	1949	Unknown ^z	Wealthy	—
Lakeland		978	1950	Malinda OP ^z	Malinda	Wealthy
Fireside		993	1943	Unknown ^z	Wealthy	Northwest Greening
Prairie Spy		1007	1940	Unknown ^z	Wealthy	Northwest Greening
Northland		1423	1957	McIntosh × Dolgo ^y	McIntosh	Dolgo
Regent		1430	1964	Daniels Red Duchess (Duchess of Oldenburg sport) × Delicious ^y	Haralson	McIntosh
Centennial		1472	1957	Dolgo × Wealthy ^y	Dolgo	Chestnut
Red Baron		1500	1970	Daniels Red Duchess (Duchess of Oldenburg sport) × Golden Delicious ^y	Duchess of Oldenburg	Golden Delicious
Keepsake		1593	1978	Frostbite × Northern Spy ^y	Frostbite	Northern Spy
Honeygold		1595	1970	Golden Delicious × Haralson ^y	Golden Delicious	Haralson
Sweet Sixteen		1630	1977	Frostbite × Northern Spy ^y	Frostbite	Northern Spy
State Fair		1639	1977	Mantet × Oriole ^y	Mantet	Haralson
Honeycrisp	Honeycrunch [®]	1711	1991	Macoun × Honeygold ^y	Keepsake	MN1627
Wildung	SnowSweet [®]	1797	2006	Connell Red (Fireside sport) × Sharon ^x	Fireside	Sharon
Minnewashta	Zestar! [®]	1824	1998	State Fair × MN1691 ^x	State Fair	MN1691
Minneiska	SweeTango [®]	1914	2006	Honeycrisp × Minnewashta ^x	Honeycrisp	Minnewashta
MN55	Rave [®]	1955	2016	Honeycrisp × AA44 (synonym MonArk) ^x	Honeycrisp	AA44
MN80	First Kiss [®] Triumph [™]	1980	2021	Honeycrisp × Liberty ^x	Honeycrisp	Liberty

^zParentage from review by Alderman et al. (1957).

^yParentage from review by Luby (1991).

^xParentage from University of Minnesota breeding records.

supported by marker data. Misidentification of trees serving as seed parents, either by UMN staff or the owners of orchards where seeds were collected (Dorsey, 1919), or mislabeling of seeds or germinated seedlings may account for incorrect seed parents. Grandparents were identified for several early cultivars even though parents remain unknown. ‘Wealthy’, which was widely grown in the Midwest United States in the late 19th and early 20th centuries (Green, 1903), was a parent of 10 of the 14 UMN cultivars introduced from 1920 through 1940 (Table 1). These include ‘Haralson’ and ‘Fireside’, which were the two most widely grown cultivars in Minnesota in the mid to late 20th century. The parentage of ‘Haralson’ was recorded as ‘Malinda’ OP. ‘Malinda’ was confirmed as a parent and the other parent was identified as ‘Wealthy’. The parentage of ‘Fireside’ was recorded as unknown, but the actual parents were confirmed as ‘Wealthy’ and ‘Northwest Greening’.

Seed from controlled pollinations provided the basis for selection as the 20th century progressed and selection was more tempered. From the late 1930s through the

2000s, only ≈600 seedlings were selected for advanced testing, resulting in the introduction of 14 cultivars (Table 1). Our results confirmed recorded parentages for 10 of the 14 cultivars. Incorrect recorded parentages for four cultivars could be elucidated. Both recorded parents of ‘Honeycrisp’ were incorrect, as previously reported (Cabe et al., 2005; Howard et al., 2017). Likewise, the recorded parents of ‘Regent’ were refuted, and ‘Haralson’ × ‘McIntosh’ was confirmed as the correct parentage. For ‘State Fair’, ‘Mantet’ was confirmed as a parent and ‘Haralson’ was identified as the other parent, rather than ‘Oriole’. For ‘Centennial’, ‘Dolgo’ was confirmed as a parent and ‘Chestnut’, rather than ‘Wealthy’, was identified as the other parent. To avoid issues with incorrect pedigrees as we have identified with past cultivars, each new selection in the UMN breeding program is genotyped on the Illumina Infinium 20K apple SNP array to confirm its identity and parentage.

Pedigree connections to important ancestors. Extended pedigrees of UMN cultivars connect to multiple important ancestors of European

and North American origin (Fig. 1). Several important founders of European apple germplasm (Muranty et al., 2020) that we identified as ancestors of the UMN breeding program include, most prominently, ‘Duchess of Oldenburg’ (synonyms ‘Borowitsky’, ‘Borovinka’, and others listed in Bussey, 2016), but also ‘Alexander’ (synonym ‘Kaiser Alexander’) and ‘Reinette Franche’.

‘Duchess of Oldenburg’ was an ancestor of overwhelming importance in the UMN breeding program (Table 1, Fig. 1). It was an ancestor of 27 of the 28 UMN cultivars, including as a parent of two cultivars and a grandparent of 15 cultivars, including ‘Honeycrisp’. ‘Duchess of Oldenburg’ was a parent of ‘Wealthy’ (Muranty et al., 2020), which was a parent of 10 of the 14 UMN cultivars introduced from 1920 through 1940. Green (1903) noted that in the late 19th century, ‘Duchess of Oldenburg’ was “the standard of hardiness in Minnesota and more generally grown than any other variety.” A sport, referred to in the UMN breeding records as ‘Red Duchess’ or ‘Daniels Red Duchess’, was used extensively as a seed parent of OP seedlings and in early controlled

Fig. 1. Extended pedigrees of University of Minnesota apple breeding program cultivars. See text for discussion of the pedigree of AA44.

crosses through the 1930s. According to Bussey (2016), ‘Daniels Red Duchess’ was selected in 1902 as a sport of ‘Duchess of Oldenburg’ at Excelsior, MN which is near the UMN Fruit Breeding Farm.

‘Duchess of Oldenburg’, along with ‘Alexander’, ‘Tetofsky’, and ‘Red Astrachan’ (the latter of which was not represented in the UMN pedigree), are noted by Bussey (2016) as four important Russian cultivars first imported to Massachusetts from England in 1835. ‘Alexander’, which Green (1903) described as “lacking in hardiness and productiveness”, contributed only to the pedigrees of two relatively obscure early 20th-century cultivars, Folwell and Redwell.

‘Tetofsky’ is an important ancestor of the early ripening UMN cultivars Beacon, State Fair, Minnewashta, Minneiska, and MN55. Compared with ‘Duchess of Oldenburg’, which was among the cultivars Green (1903) considered to be of “first degree of hardiness,” he wrote that “Tetofski [sic] is of second degree of hardiness.” However, he described it as “one of the earliest if not the earliest apple to ripen in Minnesota and should have a place in every home orchard,” although premature fruit drop prevented it from being “profitable for market.” ‘Tetofsky’ is a grandparent of ‘Beacon’, an early-ripening cultivar that was regionally popular in the mid-20th century. ‘Tetofsky’ features in the ancestry of several early-ripening Canadian-bred cultivars: Petrel, Melba, Mantet, and Goodland.

‘Petrel’ and ‘Melba’ are grandparents of ‘July Red’ (Bussey, 2016), which is likely a great-grandparent of ‘MN55’ (discussed subsequently). ‘Mantet’ and ‘Goodland’ contributed to the early-ripening UMN cultivars State Fair, Minnewashta, and Minneiska.

‘Reinette Franche’, a 16th-century cultivar from Normandy, France, and an important ancestor of European germplasm (Muranty et al., 2020), was also identified as an important ancestor of UMN cultivars through ‘Wealthy’, via its parent, ‘Jonathan’ (Fig. 1). ‘Reinette Franche’ is also an ancestor to some UMN cultivars via two other historically important U.S. cultivars, Golden Delicious and Northern Spy. Their descent from ‘Reinette Franche’ was elucidated through a concurrent large-scale apple pedigree reconstruction project (Howard et al., 2018a) and is first reported here.

In addition to European ancestors, several cultivars that were widely grown in the United States in the first half of the 20th century (Dolan, 2009) entered the UMN extended pedigree, including ‘Jonathan’, ‘Northern Spy’, ‘McIntosh’, ‘Rome Beauty’, and ‘Grimes Golden’ (Fig. 1). ‘Northern Spy’, discovered circa 1800 in western New York, was estimated by the USDA to be the third most important cultivar in the United States during the period 1909–13 (Magness, 1941). ‘Northern Spy’ was recognized for its very good eating and culinary quality as well as storage ability but required an excessively

long time to begin bearing fruit (Davis, 1925). Early UMN breeders likely sought to combine its fruit quality with the local adaptation of ‘Frostbite’ (then known as MN447). This cross gave rise to many selections, including two that were released, ‘Keepsake’, which is one parent of ‘Honeycrisp’, and ‘Sweet Sixteen’. ‘McIntosh’ appears in the pedigrees of UMN cultivars as a parent of ‘Victory’, ‘Northland’, and ‘Regent’. It is a more distant ancestor of ‘State Fair’, ‘Minnewashta’, and ‘Minneiska’ through UMN breeders’ use of Canadian cultivars, Mantet and Goodland. ‘McIntosh’ also enters the pedigree of UMN cultivar MN80 through its parent, ‘Liberty’, which contributed the allele for resistance to apple scab [*Venturia inaequalis* (Cooke) G. Winter] at the *Rvi6* locus. ‘MN80’ is the only UMN cultivar derived from the introgressive backcrossing by the cooperative Purdue–Rutgers–Illinois breeding effort (Crosby et al., 1992) that introduced resistance to apple scab into *M. ×domestica* from *M. floribunda* Siebold ex Van Houtte.

‘Delicious’, a dominant North American cultivar of the mid to late 20th century (Volk et al., 2015), was used in crossing at UMN as early as 1918 (Dorsey, 1921), yet was notably rare in the pedigrees of UMN cultivars. Although discovered in the neighboring state of Iowa (Bussey, 2016), ‘Delicious’ has not exhibited consistent fruiting and tree survival for commercial production in Minnesota except in the far southeastern corner of the state. ‘Delicious’ occurred only as a distant relative in the pedigree of ‘MN55’ through its parent, AA44, a breeding selection from the University of Arkansas that was not formally released (C. Rom, University of Arkansas, personal communication) but has been in the public domain as ‘MonArk’ since at least 1993 (Norton and Way, 1999). The parentage of AA44 is unclear from breeding records and its pedigree could not be fully elucidated in this study. Rom et al. (1998) reported that AA44 was derived from a cross between two selections from the Rutgers University breeding program, 674016 and NJ40. Breeding records at Rutgers University (J. Goffreda, Rutgers University, personal communication) indicate that the parentage of selection 674016 was PCF4-56 (‘Mollie’s Delicious’ × ‘July Red’) × NJ40 {314049 [‘Blackjon’ (sport of ‘Jonathan’) × 55737 (‘Yellow Newtown’ × ‘Edgewood’)] × 81248 [‘Jonathan’ × 11387 [‘Melba’ × (‘Williams’ × ‘Starr’)]}. None of the breeding selections, nor ‘Edgewood’, was available for genotyping, so the recorded pedigree of AA44 could not be confirmed nor denied. However, one parent of AA44 was confirmed to be a cross between ‘Mollie’s Delicious’ × ‘July Red’, suggesting that PCF4-56 was this parent. ‘Delicious’ is a great-grandparent of ‘Mollie’s Delicious’ {‘Mollie’s Delicious’ = (‘Wealthy’ × ‘Golden Delicious’) × [‘Orleans’ (‘Delicious’ × ‘Deacon Jones’) × (‘William’s Favorite’ × ‘Starr’)]} and is, thus, an ancestor of ‘MN55’, six generations removed. The haplotypes from the second

parent of AA44 were found to be completely composed of haplotypes present in 'Jonathan', 'Melba', 'Newtown Pippin', 'Starr', F2 26829-2-2, and 'Duchess of Oldenburg'.

'Malinda', although not widely grown in the United States, was frequently listed as a parent of early UMN cultivars in breeding records (Table 1). It was prized in the 19th century for its fruit appearance and long storage ability (Dorsey, 1919; Green, 1903). Dorsey (1919) recounted how seeds were collected in 1907 from trees of 'Malinda' that were topworked on 'Duchess of Oldenburg' in a private orchard in Waterville, MN, to establish seedling plantings in the new UMN apple breeding program. Dorsey (1919) noted that trees of "[Duchess of] Oldenburg, Wealthy, Scott Winter, Hiberna, English Russet, Patten Greening, Northwestern Greening, and a number of other varieties" were present in the orchard where the seeds resulting from open-pollination were collected. Cabe et al. (2005) found SSR markers did not support 'Malinda' as parent of 'Frostbite' or 'Chestnut'. We confirmed 'Malinda' was not in the pedigree of either cultivar, nor in the pedigrees of 'Folwell' and 'Minnehaha'. 'Malinda' also was not a parent of 'Beacon', although we could identify it as both a maternal and paternal grandparent. Nevertheless, 'Malinda' was an important program ancestor as a parent of three cultivars: Haralson, Lakeland, and Minjon. Through 'Haralson', 'Malinda' was an ancestor of several late 20th century cultivars (Fig. 1).

'Honeycrisp' pedigree. The extended pedigree of 'Honeycrisp' described in this study (Fig. 1) is especially relevant as it is a major U.S. cultivar, and its descendants are being introduced from breeding programs globally (Kostick and Evans, 2018, 2020). Its pedigree was previously elucidated in Howard et al. (2017). We have extended this pedigree to the ancestors 'Reinette Franche' and 'Utter's Large Red'. We also confirmed that 'Duchess of Oldenburg' is a great-great-grandparent through grandparent 'Frostbite' (Fig. 1). Although 'Honeycrisp' is unconnected to most elite apple germplasm via first-degree relationships (Migicovsky et al., 2021), the 'Reinette Franche' ancestry connects 'Honeycrisp' to a large group of European and North American cultivar descendants of 'Reinette Franche' (Muranty et al., 2020). Haplotype contributions of 'Reinette Franche' to 'Honeycrisp' were responsible for the runs of homozygosity on chromosomes 7 and 15 previously reported in Howard et al. (2017), as 'Reinette Franche' was an ancestor of both the maternal and paternal parents of 'Honeycrisp'. 'Duchess of Oldenburg' was previously speculated as a grandparent of 'Frostbite' (Howard et al., 2017). We confirmed this relationship, and thus, 'Duchess of Oldenburg' was responsible for runs of homozygosity on chromosomes 1 and 10 in 'Honeycrisp' previously reported in Howard et al. (2017). The pedigree of 'Honeycrisp's other great-great grandparent, 'Utter's Large Red' (synonym 'Utter Red', 'Utter'), a cultivar discovered in the Midwest

United States in the early 19th century (Bussey, 2016), remains unknown. It was considered by Green (1903), despite its large size, to be "entirely unworthy of planting" but was nevertheless a contributor to 'Honeycrisp'.

Conclusion

Using genomics and informatics technologies, we were able to construct extended, connected pedigrees for cultivars introduced from a breeding program that has continuously developed germplasm for more than a century. Parentage was confirmed for most cultivars introduced in the late 20th and early 21st century and was discovered for many cultivars from the early 20th century when breeding records were often incomplete or incorrect. These elucidated pedigrees confirmed the importance of 'Duchess of Oldenburg' as an important ancestor, possibly providing improved adaptation to the continental climate of the region. Identification of genomic contributions from 'Duchess of Oldenburg' that are conserved in its selected descendants from early cultivars through to present selections in the UMN breeding program may highlight regions to target for future selection. This approach could be used for other clonally propagated crops where provenance information and comprehensive, carefully curated SNP array data are available for older germplasm, such as cherry [*Prunus avium* (L.) L.] or peach [*P. persica* (L.) Batsch] (Vanderzande, et al., 2019). Corrected and confirmed parentages based on DNA markers are useful for germplasm managers holding these cultivars in their collections as well as nurseries and apple growers who feature cultivar parentage in describing their products. Extended pedigrees will be useful to breeders in constructing future crosses to reduce or increase inbreeding and identify cultivars that are putative carriers of desirable or undesirable alleles based on their ancestry (Howard et al., 2018b). Examining the pedigrees in conjunction with historical documents provides insights into the strategies of earlier breeders and helps describe the arc of development for a breeding program with a long history.

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Supplemental Table 1. Meta-data for University of Minnesota apple breeding program cultivars and accessions of their ancestors. The individuals used in the study were cataloged by MUNQ codes (for Malus UNiQue genotype codes; Denancé et al., 2020) which were defined to facilitate international comparison of apple genetic resources as a development from the FBUNQ code described by Urrestarazu et al. (2016) based on SSR marker data. Individuals with the same MUNQ code are genotypic duplicates. These accessions are part of a large MUNQ code dataset (Denancé et al., 2020). Individuals that lacked SSR data and thus typical MUNQ attribution were given provisional MUNQ codes, typically derived from accession id numbers.

Analysis_Name	Accession_ Name	Accession_ID	Accession_ Source_ Organization	Accession_ Source_ Country	SNP_data_Source	MUNQ
Beacon	Beacon	USA_UMN0041	UMN	USA	University of Minnesota apple breeding program	12
Ben_Davis	Ben Davis	PI_588953	PGRU-Geneva	USA	Fruit_Breedomics	106
Centennial_Crab	Centennial Crab	USA_UMN0009	UMN	USA	University of Minnesota apple breeding program	USA_UMN0009
Chestnut_Crab	Chestnut Crab	USA_UMN0042	UMN	USA	University of Minnesota apple breeding program	USA_UMN0042
Deacon_Jones	Deacon Jones	USA_TOC_3702714	The Temperate Orchard Conservancy	USA	From the project described in Howard et al., 2018a	USA_TOC_3702714
Delicious	Oetwiler Renette	PI_134809	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	448
Dolgo	Dolgo	PI_588870	PGRU-Geneva	USA	Fruit_Breedomics	FEM_1_23
Duchess_of_Oldenburg	Borowsky	X00048	INRAE	France	Fruit_Breedomics	29
Esopus_Spitzenburg	Esopus Spitzenburg	X01094	INRAE	France	Fruit_Breedomics	522
F2_26829_2_2	F2-26829-2-2	FBo_WP3_0215	University of Bologna	Italy	Fruit_Breedomics	1479
Fameuse	Snow	PI_588793	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	303
Fireside	Fireside	USA_UMN0010	UMN	USA	University of Minnesota apple breeding program	2902
Folwell	Folwell	USA_UMN0003	UMN	USA	University of Minnesota apple breeding program	USA_UMN0003
Frostbite	Frostbite	USA_UMN0007	University of Minnesota	USA	University of Minnesota apple breeding program	USA_UMN0007
Golden_Delicious	Nugget	PI_589430	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	65
Golden_Russet_1	Golden Russet	PI_589892	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	2862
Goodland	Goodland	PI_590158	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	8032.1
Grimes_Golden	Grimes Golden	PI_588791	PGRU-Geneva	USA	Fruit_Breedomics	3190
Haas	Haas	USA_SSE0014	Seed Savers Exchange	USA	From the project described in Howard et al., 2018a	USA_SSE0014
Haralson	Haralson	FBo_WP3_0198	Warsaw University of Life Sciences	Poland	Fruit_Breedomics	1062
Honeycrisp	Honeycrisp	USA_UMN0001	UMN	USA	University of Minnesota apple breeding program	1489
Honeygold	Honeygold	FBo_WP3_0170	Research Institute of Horticulture	Poland	Fruit_Breedomics	1063
Jersey_Black	Jersey Black	1952130	National Fruit Collection	United Kingdom	From the project described in Howard et al., 2018a	2856
Jonathan	Jonathan	FBo_WP3_0348	Wageningen University of Research	The Netherlands	Fruit_Breedomics	57
Julyred	Julyred	FBo_WP3_0005	Agroscope Changins Waedenswil	Switzerland	Fruit_Breedomics	1033.3
Alexander	Alexander	PI_589107	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	30
Keepsake	Keepsake	USA_UMN0023	UMN	USA	University of Minnesota apple breeding program	2655
Keswick_Codlin	Keswick Codlin	2000053	National Fruit Collection	United Kingdom	Muranty et al., 2020	1438
Lakeland	Lakeland	USA_UMN0046	UMN	USA	University of Minnesota apple breeding program	2900
Liberty	Liberty	FEM_1_34	Fondazione Edmund Mach	Italy	Fondazione Edmund Mach	585
Glogerovka	Pepinka Litowska	PI_589116	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	1041
Suislepper	Lowland Raspberry	USA_SSE0057	Seed Savers Exchange	USA	From the project described in Howard et al., 2018a	239
M_floribunda_821	Malus floribunda #821	FBo_WP3_0219	University of Bologna	Italy	Fruit_Breedomics	998
Macoun	Macoun	DEU_JK1_MD_0395	Julius Kühn Institute	Germany	Fruit_Breedomics	1055.3
Malinda	Malinda	PI_644176	PGRU-Geneva	USA	Fruit_Breedomics	PI_644176
Mantet	Mantet	PI_589367	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	603
McIntosh	McIntosh	X00557	INRAE	France	Fruit_Breedomics	508
Melba	Melba	CRAW-0836	Walloon Agricultural Research Center	Belgium	Fruit_Breedomics	167

(Continued on next page)

Supplemental Table 1. (Continued)

Analysis_Name	Accession_ Name	Accession_ID	Accession_ Source_ Organization	Accession_ Source_ Country	SNP_data_Source	MUNQ
Minjon	Minjon	DEU_JKI_MD_0680	Julius Kühn Institute	Germany	Fruit_Breedomics	1432.2
Minnehaha	Minnehaha	PI_589030	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	2907
Minneiska	Minneiska	USA_UMN_MN1914	UMN	USA	University of Minnesota apple breeding program	USA_UMN_MN1914
MN1627	—	—	—	—	Howard et al., 2017	(not assigned)
MN1691	MN1691	USA_UMN0008	UMN	USA	University of Minnesota apple breeding program	USA_UMN0008
MN80	MN80	USA_UMN_MN1980	UMN	USA	University of Minnesota apple breeding program	(not assigned)
MN55	MN55	USA_UMN_MN1955	UMN	USA	University of Minnesota apple breeding program	USA_UMN_MN1955
Mollies_Delicious	Mollies_Delicious	PI_588981	PGRU-Geneva	USA	Fruit_Breedomics	2703
Monark	Monark	USA_UMN0002	UMN	USA	University of Minnesota apple breeding program	USA_UMN0002
Newtown_Pippin	Yellow Newtown	PI_588773	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	787
Northern_Spy	Northern Spy	FBo_WP3_0199	Warsaw University of Life Sciences	Poland	Fruit_Breedomics	23
Northland	Northland	PI_589718	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	PI_589718
Northwest_Greening Oriole	Northwest Greening Oriole	PI_589896 USA_UMN0031	PGRU-Geneva UMN	USA USA	Fruit_Breedomics University of Minnesota apple breeding program	6673.1 698
Orleans	Orleans	PI_276567	PGRU-Geneva	USA	Fruit_Breedomics	249
Pattens_Greening	Pattens Greening	USA_SSE0068	Seed Savers Exchange	USA	From the project described in Howard et al., 2018a	USA_SSE0068
Prairie_Spy	Prairie Spy	PI_589898	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	2901
PRI_54_12	PRI 54-12	FBo_WP3_0109	Julius Kühn Institute	Germany	Fruit_Breedomics	FBo_WP3_0109
Red_Baron	Red Baron	USA_UMN0088	UMN	USA	University of Minnesota apple breeding program	2302
Redwell	Redwell	USA_UMN0006	UMN	USA	University of Minnesota apple breeding program	2899.2
Regent	Regent	USA_UMN0033	UMN	USA	University of Minnesota apple breeding program	2680
Reinette_Franche	Reinette Franche	PI_590137	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	278
Scotts_Winter	Scotts Winter	USA_SSE0074	Seed Savers Exchange	USA	From the project described in Howard et al., 2018a	USA_SSE0074
Sharon	Sharon	USA_SSE0086	Seed Savers Exchange	USA	From the project described in Howard et al., 2018a	3184.2
Spasovka_Kvasna	Spasovka Kvasna	PI_307518	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	7867
Starr	Starr	1952118	National Fruit Collection	United Kingdom	From the project described in Howard et al., 2018a	2395
State_Fair	State Fair	USA_UMN0032	UMN	USA	University of Minnesota apple breeding program	2614.2
Sweet_Sixteen	Sweet Sixteen	USA_UMN0026	UMN	USA	University of Minnesota apple breeding program	1047
Tetofsky	Tetofsky	USA_TOC_1003311	The Temperate Orchard Conservancy	USA	From the project described in Howard et al., 2018a	USA_TOC_1003311
Utters_Large_Red	Utters Large Red	USA_SSE0108	Seed Savers Exchange	USA	From the project described in Howard et al., 2018a	USA_SSE0108
Victory	Victory	USA_UMN0049	UMN	USA	University of Minnesota apple breeding program	2898.2
Wealthy	Williams	PI_589133	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	6
Wedge	Wedge	PI_589190	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	PI_589190
Wildung	Wildung	USA_UMN0030	UMN	USA	University of Minnesota apple breeding program	USA_UMN0030
Williams_Favourite	William's Favorite	1957233	NFC	United Kingdom	Fruit_Breedomics	591
Yellow_Bellflower	Turkish Sour Apple	PI_686986	PGRU-Geneva	USA	From the project described in Howard et al., 2018a	77
Minnewashta	Minnewashta	USA_UMN0029	UMN	USA	University of Minnesota apple breeding program	5427