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# 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 'Borowitsky') 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, Minneota'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 Sätra 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®<br>Triumph™ | 1980 | 2021 | Honeycrisp × Liberty[x] | Honeycrisp | Liberty |

[z] Parentage from review by Alderman et al. (1957).

[y] Parentage from review by Luby (1991).

[x] Parentage 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

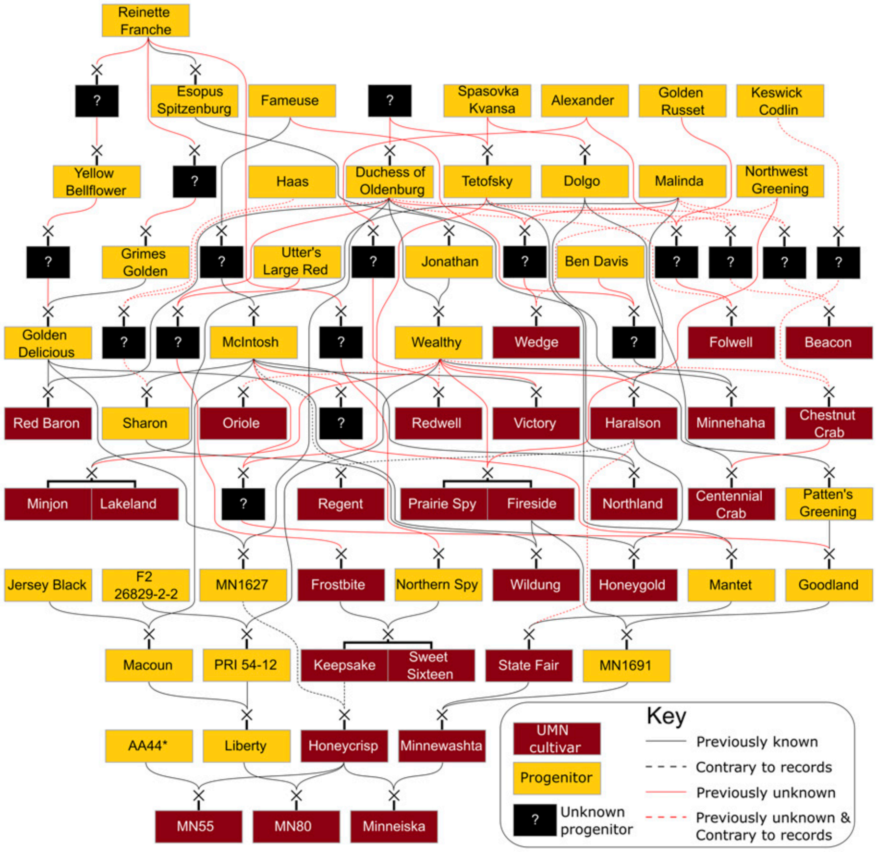

Fig. 1. Extended pedigrees of University of Minnesota apple breeding program cultivars. See text for discussion of the pedigree of AA44.

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, Hibernal, 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 | Borowitsky | 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_JKI_ 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 | Northwest Greening | PI_589896 | PGRU-Geneva | USA | Fruit_Breedomics | 6673.1 |
| Oriole | Oriole | USA_UMN0031 | UMN | USA | University of Minnesota apple breeding program | 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 |