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Unlocking heirloom diversity: a pathway to bridging global challenges in modern apple cultivation

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Reports indicate that climate changes will result in the extinction of a significant percentage of plant species even though many of these species contributed to crucial genetic traits that led to the development of domestic crops. In the past, the diversified range of plant species, varieties, and agricultural practices allowed agriculture production and local food systems to tolerate moderate climate variability. Today, industrial farming relies on very limited genetic diversity for commercial production. Narrowing the genetic base leads to higher susceptibility to environmental changes and diseases.

Heirloom cultivars survived climate variations and extreme conditions but were abandoned in favor of a handful of commercial cultivars that dominate the food industry and fit the standards of the global food system. From a climate change perspective, it would be important to conserve heirloom cultivars to preserve biodiversity and make greater genetic diversity available to farming, which will lead to resilience and adaptation.

KEYWORDS

heirloom, apples, biodiversity, genetic erosion, climate change, pest pressure, fruit quality

1 Introduction

The apple (*Malus domestica*) is one of the most economically important fruits cultivated in temperate areas (Yuri et al., 2019), ranking 3rd in fruit production (Statista, 2021) and 17th among all agricultural commodities (Volk et al., 2015). However, global apple production for 2022/2023 declined by 4.3 million metric tons (tonnes) to 78.4 million due to weather-induced losses (USDA, 2023).

Originally from Central Asia, apples were introduced to Europe and later spread to other continents, resulting in the description of more than 20,000 ancient cultivars (Yuri et al., 2019). While industrialized farming systems have increased production and provided a uniform yield, they have significantly contributed to genetic erosion and the loss of biodiversity. The apple industry is now dominated by a handful of commercial cultivars that fit the standards of the global food system. This loss of biodiversity occurred due to the expansion of commercial agriculture, narrowing down apple production to very few cultivars, such as 'Golden Delicious,' 'Gala,' 'Fuji,' and 'Granny Smith' (Piccolo et al., 2019).

The challenges posed by climate variability, the increased risks of pest infestations, socioeconomic factors, and the continual depletion of natural resources raise significant concerns regarding the sustainability of apple production and its resilience against external factors, especially if there is a persistent decline in genetic diversity.

In this review, we first describe key challenges confronting apple production, underscoring the repercussions of relying on a very limited number of modern-day cultivars developed to fit specific standards of commercial agriculture and food systems. In the subsequent section, we emphasize the potential of heirloom apple biodiversity—referring to the richness of older or traditional apple varieties passed down through generations and often underutilized in large-scale agriculture—to contribute to more sustainable and resilient production, provided these varieties are preserved and propagated.

2 Challenges facing modern-day cultivated apples

2.1 Genetic erosion and loss of diversity

Genetic erosion manifests as the loss of genetic diversity within the cultivated apple population. Over time, the genetic foundation of cultivated apples has significantly changed (Marconi et al., 2018). In the past, numerous regional and local apple varieties were maintained through clonal propagation. Nowadays, the market primarily offers a few selected and related cultivars that meet the preferences of growers, customers, and retailers (Hokanson et al., 1997; Marconi et al., 2018), leading to a decline in genetic diversity for domesticated apples. In the 19th century, more than 7,000 commercial cultivars were known, but today, the world's production relies heavily on only a handful of major cultivars, such as 'Golden Delicious' and 'Delicious' and its red sports (Hokanson et al., 1997).

The loss of crop genetic diversity can be attributed to several factors, including environmental changes, labor market shifts, and civil conflicts. However, the dominance of modern cultivars over traditional ones in most areas has been the primary cause (Goland and Bauer, 2004). Modern commercial agriculture favors high-yielding uniform cultivars, resulting in the abandonment of 80%-90% of fruits and vegetables during the 20th century (Testolin et al., 2019). Monocropping systems, with genetically uniform super producers, require intensive labor and inputs like pesticides, irrigation, and fertilizers, leading to a vulnerable agricultural landscape. A single adverse event, such as a climate event, disease outbreak, or pest infestation, can devastate these systems (Testolin et al., 2019).

Commercial agriculture demands consistent ripening times, prolonged storage life, and high-quality produce for shipping and processing, leading to a reduction in fruit diversity. Family orchards, known for producing apple cultivars with diverse flavors, textures, and sizes, have been replaced by a limited number of cultivars that fit the global market standards (Goland and Bauer, 2004; Jakobek et al., 2020).

Today, the global fruit-breeding industry produces a wide range of cultivars, but many modern cultivars have limited ancestry, stemming from just a few ancestor varieties in their breeding lines. In the case of apple hybrids developed since 1920, most can be traced back to six ancestors: 'Golden Delicious,' 'Cox's Orange Pippin,' 'Jonathan,' 'McIntosh,' 'Red Delicious,' and 'James Grieve' (Bannier, 2011; Mădălina et al., 2022). This over-reliance on a small set of ancestors has led to genetic impoverishment, a decrease in effective population size, and a reduction of the overall fitness and health of the offspring, a phenomenon termed inbreeding depression (Bannier, 2011; Dan et al., 2015).

2.2 Limited availability and accessibility

The access of industrialized agriculture to global markets has led to a decline in the diversity of apple cultivars available for farming. The farther food travels and becomes integrated into global supply chains, the more pronounced the reduction in crop biodiversity becomes (Goland and Bauer, 2004). Local markets preserved heirloom cultivars grown by farmers according to their own standards rather than conforming to global market demands. But the globalization of food supply transformed the role of farmers from responsive entrepreneurs catering to local consumers into mass marketers of generic commodities (Halweil, 2002), resulting in the disappearance of many heirloom apple cultivars (Anastopoulo, 2014). Currently, an average of 10 to 20 cultivars out of 7,500 named varieties dominate the market (Volk et al., 2015).

Initially, cultivars were treated as common goods and further developed by farmers, leading to rich agrobiodiversity. However, with the industrialization of agriculture, the breeding process shifted to professional institutes, focusing on standardized cultivars for large-scale cultivation and mass markets. This transformation turned seeds and varieties from common goods to private goods (Wolter and Sievers-Glotzbach, 2019).

Moreover, access to and distribution of new apple cultivars have become exclusive and limited, with many newly bred cultivars being privatized through club concepts. These protected cultivars are only available to selected farmers who meet specific criteria (Hanke and Flachowsky, 2017). However, most of the regularly introduced apple cultivars fail to gain widespread market acceptance because either they show undesired traits in productivity or fruit quality after a few years of cultivation, or market demand is too low (Wolter and Sievers-Glotzbach, 2019; Hanke and Flachowsky, 2017; Hanke et al., 2020).

The narrowing genetic base of modern apple cultivars results in reduced genetic variance, lower vigor, and a prolonged juvenile period. This increased uniformity makes these cultivars more susceptible to environmental changes, vitality problems, and pest susceptibility (Dan et al., 2015).

2.3 Pest pressure and resistance breakdown

Modern-day apple cultivars are susceptible to a wide range of pests and pathogens (Volk et al., 2015). To drastically limit the spread of pests and diseases and maintain marketable yield, farmers rely on regular and heavy use of pesticides that can range from 10 to 18 spray applications per growing season (Balint et al., 2013).

Plant protection products are constantly used in both breeding programs and farming to suppress scab and other diseases on modern trees and fruits. Apple scab, *Venturia inaequalis*, is one of the most devastating fungal diseases affecting apples, causing significant economic losses in many cultivated areas. In the absence of effective control measures, losses can reach up to 70% (Shafi et al., 2019). Although disease incidence can be minimized by implementing an integrated pest management approach, fungicides are heavily used as the primary control measure (Choupannejad et al., 2018). This poses an issue as the usage of synthetic chemical fertilizers and pesticides negatively affects ecosystems and the overall sustainability of agriculture (Power, 2010).

After identifying a number of resistant genes, the gene *Rvi6* (*Vf*), derived from a cross with one wild apple, *Malus floribunda* 821, became the most common source of resistance to apple scab (Baumgartner et al., 2015; Choupannejad et al., 2018). Since 1970, approximately 80% of scab-resistant apple cultivars released worldwide reportedly carry the major resistance gene *Rvi6* (*Vf*). This dependency on a single gene from one ancestor not only caused genetic impoverishment but also led to the breakdown of resistance by the causal fungal agent. Apple scab fungal races 6 and 7, capable of overcoming *Vf* resistance, emerged, and a complete breakdown of resistance was discovered in apple scab isolates in Europe and the United States, highlighting the need for polygenic sources of resistance (Baumgartner et al., 2015; Papp et al., 2020). This proves that a single major resistance gene is not the ideal solution to reduce disease pressure.

2.4 Climate alterations and variability

Climate change poses a serious threat to the productivity of fruit trees, particularly apples, grown in temperate regions (Osborn and Briffa, 2006; Rai et al., 2015). Apples are perennial tree crops with a productive lifespan ranging from 20 to 100 years, making them susceptible to environmental variations (Veteto and Carlson, 2014). Climatic parameters such as temperature, CO_2 levels, and rainfall patterns impact the proper development and yield stability of fruit trees. Climatic data have recorded warmer winters, advanced spring phenology, and extreme weather events like frosts, hailstorms, heavy rains, and droughts in comparison with the pre-industrial period (IPCC: Intergovernmental Panel on Climate Change, 2021; Ahmadi et al., 2019; Veteto and Carlson, 2014). These variations and events affect the phenological stages of fruit tree crops and aggravate the incidence of insects and disease infestations. The variations in the timing of phenological stages of fruit trees can significantly impact the economy by directly influencing productivity, thereby affecting the final crop yield (Chmielewski et al., 2004).

Numerous studies have been conducted on fruit tree crops to assess the implications of climate change on the timing and duration of phenological stages, with apples being important indicators (Veteto and Carlson, 2014). For instance, the highly sensitive bloom time, occurring in spring before fruit set, is correlated with air temperature (Veteto and Carlson, 2014). An increase of 1°C in average air temperature between February and April in Germany resulted in advancing the flowering date by 5 days (Chmielewski et al., 2004). Similarly, records of temperature and phenological events in six locations in Japan showed an advance in apple phenology correlated with the long-term trend increase in air temperature (Fujisawa and Kobayashi, 2010). Studies have shown that the most important temperature increase in winter and spring, occurring between January and April, results in earlier flowering. This coincides with the spring frost timing, posing risks of frost damage for apple flowers in certain regions (Blanke and Kunz, 2011; Kunz and Blanke, 2022).

Warmer winters have been linked to advancements in blooming and an increased risk of frost damage. Early-blooming varieties, like the well-known 'Red Delicious,' have suffered severe losses due to spring freezes (Veteto and Carlson, 2014). Changes in temperature are perceived as the most threatening because they not only affect phenological stages but also external and internal apple quality (Musacchi and Serra, 2018). Chilling requirements of apples, essential for their complete growth, are likely to be affected by increasing temperatures, raising concerns about the future feasibility of certain cultivars (Rai et al., 2015; Funes et al., 2016).

In response to a changing climate, alterations in the taste and textural qualities of apples have been observed in Japan over a period of 30 years–40 years. The leading apple cultivar 'Fuji' showed significant decreases in firmness, organic acid concentration (sourness), and storage stability, attributed to earlier blooming and higher temperatures during the maturation period (Sugiura et al., 2013). Other disorders in apples linked to market traits, such as reduced fruit size, unmarketable color, and shorter shelf life, have been attributed to climate change (Singh et al., 2016).

The effects of environmental changes are not limited to scientific data but are also documented from the perspective of apple farmers. In Appalachian North Carolina, one of the earliest orchard areas in the United States, 22 experienced apple orchard managers recognized higher frequencies of frosts and hailstorms. These weather conditions contribute to an increased incidence of diseases and insect pests, primarily fire blight, apple scab, and spider mites, resulting in devastating losses in apple production (Veteto and Carlson, 2014; Singh et al., 2016).

3 Potential of heirloom varieties

3.1 Vitality against major pests

Heirloom apple varieties possess a robust genetic background that grants them high tolerance to major modern-day apple diseases. They have adapted to various climates and soils over time, showcasing their resilience against diseases, making them valuable for apple breeding (Wichmann et al., 2007). Notably, Papp et al. (2016) found resistance against apple scab and powdery mildew in heirloom cultivars in Hungary, which likely comes from multiple genes. With the rise of apple scab due to climate change factors (such as increased leaf wetness and humidity), maintaining heirloom varieties with diverse defense mechanisms becomes important to provide polygenic sources of resistance for breeders and growers alike (Sharma and Bhandari, 2018).

Heirloom varieties also show resistance to blue mold decay (*Penicillium expansum*), a significant post-harvest threat to apples (Sun et al., 2017). Wild apple germplasm from the center of origin in Kazakhstan displayed resistance to this disease (Jurick et al., 2011). Moreover, highly resistant wild apples discovered in 2015 indicated new resistance mechanisms, linked to phenolic compounds that were more abundant in heirloom varieties (Sun et al., 2017).

Controlling the serious pest fire blight (*Erwinia amylovora*) in apples is costly (Volk et al., 2015). Despite control measures, management remains complex due to the development of resistant bacterial strains (Zhao et al., 2019). Heirloom apple varieties in multiple countries exhibit high resistance (Tóth et al., 2013; Ozrenk et al., 2011; Korba et al., 2008; Nybom et al., 2012).

Comparing heirloom and modern cultivars in Germany for more than 15 years, Bannier (2011) found heirloom cultivars to be more vital, emphasizing their genetic diversity. Focusing on overall apple tree health and genetic diversity highlights the potential of heirloom varieties to improve resistance and vitality in modern apple cultivation.

3.2 Climate hardiness and suitability for organic farming systems

Historically, a diversified range of species, varieties, and practices allowed agricultural production to tolerate moderate climate variability. Heirloom cultivars, well-suited to local climate conditions, resulted from centuries of farmers' practices, observations, and selection (Lane and Jarvis, 2007). In the past, each country and region produced apple cultivars adapted to the local climate, contributing to their resilience (Janick and Moore, 1996).

Heirloom apples are well suited for organic farming systems due to their resilience and vigor, offering practical and cost-effective solutions to major pests that pose challenges in organic agriculture (Volk et al., 2015). Some heirloom cultivars have demonstrated high-to-moderate resistance to major apple diseases without the need for chemical interventions (Aoun, 2013; Balint et al., 2013).

Moreover, heirloom cultivars not only offer climate hardiness and natural tolerance to pests but also hold promise for their superior nutritional characteristics (Akagić et al., 2019; Jakobek et al., 2020). Some heirloom apple cultivars have been found to have higher trace elements, mineral content, and phosphates in their juices and disease-induced resistance phenolic compounds (Singh et al., 2016; Kschonsek et al., 2018; Oras et al., 2023). Additionally, some heirloom varieties possess desirable and attractive flavor and textural traits, making them potentially suitable for commercial cultivation (Aoun, 2013; Jakobek et al., 2020).

Furthermore, regional heirloom cultivars boast a genetic background conducive to breeding for organic and low-input systems. Breeding for such systems, emphasizing vitality and reduced vulnerability to major diseases (Ristel et al., 2016), recognizes certain heirloom varieties exhibiting high disease tolerance and simultaneously producing quality apples (Wichmann et al., 2007). Heirloom cultivars can be further improved and bred for productivity and unique traits under organic conditions, making them ideal for such farming systems.

3.3 Preservation of heirloom apple heritage and germplasm

Local food systems play a crucial role in promoting heirloom varieties and preserving biodiversity (Goland and Bauer, 2004). As new consumption trends drive an increasing demand for organic and local produce, consumers are motivated to support their heritage, local communities, and the environment by buying from local markets (Dinis et al., 2011; Donno et al., 2012). Studies even show that consumers are willing to pay higher prices for local varieties (Denver and Jensen, 2014).

Apples hold great significance in a country's food traditions and orchard heritage, making their conservation vital to preserving the nation's history. Public awareness has grown, prompting the search for heirloom varieties to reintroduce them to local communities. The dominance of a few apple cultivars puts around 90% of traditional apple varieties in the United States at risk of extinction, driving initiatives like the Renewing America's Food Traditions (RAFT) Alliance to discover and reintroduce 90 traditional apple cultivars to regional orchards, nurseries, and restaurants.

In the United Kingdom, where 81% of traditional apple orchards have vanished, conservationists are planting British heritage varieties in community plots (Miller, 2022). Similarly, in Canada, efforts have been made toward the identification, propagation, and assessment of heirloom apple trees in Quebec (Aoun, 2013; Villeneuve-Desjardins et al., 2019). Also, the Heritage Apple Project in Ontario collects leaf samples from residents to genetically identify historical trees and preserve them for future generations.

Governmental and scientific efforts to preserve heirloom cultivars include the establishment of *ex situ* gene banks globally and the genetic characterization of the apple germplasm collections to increase the genetic diversity useful for modern breeding programs (Marconi et al., 2018; Skytte af Sätra et al., 2020). However, gene banks face challenges like inadequate funding, limited documentation, and environmental threats. To combat this, the United States Department of Agriculture (USDA) suggests a global strategy that combines *ex situ* gene banks, on-farm conservation efforts, and farmer communities to ensure the long-term sustainability of ancient apple cultivars. While *ex situ* conservation has limitations due to governmental restrictions, *in situ* conservation by indigenous seed savers and farmers who grow heirloom apples for local markets plays a crucial role in preserving these cultivars. Linking *ex situ* and *in situ* conservation is essential for the effective preservation of heirloom apples (Zhu et al., 2003; Bramel and Volk, 2019; Dwivedi et al., 2019).

4 Conclusion

After being excluded from the market due to their limitations, heirloom cultivars are regaining interest from scientists and breeders who recognize their genetic diversity as key to future food security, breeding programs, and production. Current global challenges and the loss of genetic vitality in modern-day dominant cultivars necessitate rapid and global cooperation of governments, private entities, and local farming communities to ensure effective long-term preservation and utilization of the remaining heirloom apple cultivars. Additionally, local markets should expand along with commercial markets as they promote heirloom cultivars and create additional income for farmers. The diversity of apple germplasm in *ex situ* gene banks must be matched with a similar increase of apple cultivars being available for farmers and in the market.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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