

Chapter

The Contribution of *Malus sieversii* to the Emergence and Diversity of Domesticated Apple Varieties

Aisha Taskuzhina, Alexandr Pozharskiy and Dilyara Gritsenko

Abstract

The modern apple is a result of hybridization between wild apples and various landraces, with the genetic composition of *Malus domestica* being primarily shaped by the hybridization of wild species *M. sieversii*, *M. baccata*, *M. orientalis*, and *M. sylvestris*. The genetic purity of wild apple populations before and after domestication is a concern. *Malus sieversii* is the primary progenitor of modern apples, with 46% of the *M. domestica* genome originating from this species. Despite facing harsh environmental conditions, the species has continuously adapted, developing genetic resistance to both abiotic and biotic factors. This resilience makes it a valuable source for breeding purposes. The population analysis of *M. sieversii* in Kazakhstan indicates substantial genetic variety; yet there is a notable prevalence of gene flow from cultivated to wild apple populations. This hybridization process is likely intensifying the extinction risk faced by wild progenitors of apples, posing a threat to biodiversity preservation and hindering efforts to improve apple varieties, including enhancing resistance to abiotic stress and optimizing production capabilities.

Keywords: wild apple, *Malus sieversii*, genetic diversity, conservation, apple cultivars

1. Introduction

The wild apple species *Malus sieversii*, which is naturally occurring in Central Asia, is widely recognized as the original ancestor of the domesticated apple *Malus domestica* [1]. *Malus sieversii* is distributed in the mountainous regions of Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan, and China, where it thrives under a wide range of ecological conditions. The genetic diversity of *Malus sieversii* has played a significant role in the development of the several apple cultivars prevalent today. The genetic diversity of this species has served a vital role in contributing features, such as resistance to diseases, large fruit size, desirable flavor, and ability to withstand environmental pressures. These traits are essential for the creation and long-term viability of modern apple cultivars [2].

The Sievers apple tree was named after the scientist and pharmacist, member of the Imperial Academy of Sciences and the Free Economic Society in St. Petersburg, Johann Sievers, who first discovered and described these wild apple trees in the

Urdzhar River valley during his expedition to Altai, Siberia and Central Asia in 1792–1794. In his letters, which were posthumously published by P. S. Pallas in 1796, he wrote: “When I arrived at the foot of the mountain, the goddess Flora delighted me with a forest of the most beautiful dwarf apple trees, which grow wild here at Urdzhar on both banks. I forgot my fatigue, the heat, the rockfall, and everything else and entered the apple trees like a wood sprite and began to feast. Forgive me for this exuberance; you know, I was born in the land of apples. During my 4 years in Siberia, I have not tasted other fruits, except for the wild pears growing beyond Lake Baikal, which are eaten there as a dessert with powdered sugar instead of candies. But those I found now were a good tart fruit, though here, in their wild state, they have shrunk to the size of a bee’s egg and have red and yellow cheeks. In Kyrgyz, they are called ‘alma’. It seems one could present this variety as a new species. The three Siberian peasants who were with me were even more amazed. They had heard from their fathers, who came from Little Russia and Poland, frequent mentions of the abundance of apples there, but they had never seen any themselves” [3]. Baltic German botanist Carl Friedrich von Ledebour conducted an expedition to the Altai and Eastern Kazakhstan (Tarbagatai) and in his book “Flora Altaica” provided a detailed description of *Malus sieversii*, naming it in honor of Johann Sievers [4]. Russian and Soviet agronomist, botanist, and geneticist, who identified the centers of origin of cultivated plants Nikolai Vavilov during his expedition to Kazakhstan noted that the wild apple trees of Central Asia are characterized by relatively large fruits, and some trees bear fruits that are comparable in quality to cultivated forms. This led him to suggest that Central Asian region is the center of origin for apple cultivation [5]. Academician Aimak Dzhangaliev, the follower of Nikolai Vavilov’s research, provided further evidence and expanded on the theory that Central Asia is the primary location where the apple tree originated. He discovered distinct populations of *Malus sieversii* in Kazakhstan, particularly in the mountainous regions of the Dzungarian Alatau, as well as in the Tian Shan. Dzhangaliev conducted research on the genetic variability and resistance of wild apple trees to different diseases, resulting in a substantial contribution to apple breeding programs and the preservation of apple genetic resources. His research significantly advanced the comprehension of the significance of conserving the wild progenitors of cultivated plants to guarantee food security and develop sustainable agriculture in the future [6, 7].

In 1989, 1993, 1995, and 1996, the U.S. Department of Agriculture (USDA)-Agricultural Research Service (ARS)-National Plant Germplasm System (NPGS) organized four expeditions to Central Asian countries. The expedition was mainly conducted in Kazakhstan in collaboration with Aimak Dzhangaliev. A total of 892 *Malus sieversii* samples were collected over four expeditions from 12 regions in Central Asia. Specifically, samples were collected from nine regions in Kazakhstan and one region each in Kyrgyzstan, Uzbekistan, and Tajikistan. The extensive collections have contributed to a deeper understanding of the genetic variation and evolutionary history of *Malus sieversii*. Seedlings have undergone studies in different countries, such as in the United States, Canada, South Africa, New Zealand, Norway, and Germany [8, 9]. The accessions have played a pivotal role in numerous research, encompassing genetic mapping, trait analysis, and breeding programs, with the objective of enhancing disease resistance and environmental adaptability in cultivated apple varieties. The research undertaken using these collections has emphasized the importance of *Malus sieversii* as a crucial genetic resource for apple production worldwide. Advanced scientific methods, including genome sequencing and molecular markers, have allowed us to gain a more profound understanding of the genetic composition and

variety of this species. Furthermore, these investigations emphasize the necessity of ongoing conservation efforts to protect these invaluable genetic resources from concerns, such as habitat degradation and climate variability.

This chapter will examine the important role of *Malus sieversii* in the development and variety of domesticated apple species. We will analyze the genetic knowledge acquired from these collections, its influence on modern apple breeding, and the continuous efforts to conserve this crucial species. By comprehending the significance of *Malus sieversii*, we may enhance our grasp of the genetic basis of cultivated apples and the necessity of preserving its wild relatives.

2. Genetic and ecological significance

2.1 Natural habitat and ecological adaptations

Malus sieversii thrives in a wide range of ecological conditions, from the Tian Shan high regions with their prolonged and severe winters to the more temperate foothills and lowlands. They have the ability to withstand a broad variety of temperatures, making them capable of enduring cold winters and hot summers. *Malus sieversii* is distributed in many habitats, such as forests, mountain slopes, and river valleys, characterized by a wide range of soil conditions, ranging from fertile with high organic content to stony and nutrient poor. This apple tree is able to adapt to different levels of water availability, allowing it to efficiently use water from snowmelt and seasonal rainfall in mountainous areas, as well as survive in drier foothills and lowlands. They also serve as crucial food sources for wildlife and provide habitat and shelter for various organisms. By enabling its ability to overcome various environmental conditions, this species is highly important for conservation and breeding efforts that aim to enhance the genetic diversity of cultivated apples [6, 7].

Malus sieversii grows in the mountain systems of the Tian Shan, Dzhungarian Alatau, Altai, and Pamir-Alai in the territory of Central Asia and China at altitudes ranging from 500 to 1900 meters. This wide range of altitudes demonstrates its adaptability to different atmospheric pressures and oxygen levels, which vary significantly with altitude. In China, it is found in the Xinjiang Uygur Autonomous Region in the western Tian Shan Mountains and in Altai (the southern region of the Tarbagatai) [10]. In Kazakhstan, wild apple is distributed mainly in the Zhongar Alatau and the western regions (Karatau and Talas Alatau) and northern regions (Ile-Alatau and Kyrgyz Alatau) of Tian Shan, with a small presence in the Altai (Tarbagatai) mountain systems. In Kyrgyzstan, *Malus sieversii* is primarily distributed in the northern, western, and central parts of the Tian Shan Mountains, specifically within the Fergana Range and the Alai Range, as well as the foothills of the Kyrgyz Alatau. In Tajikistan, the species is found in the Pamir-Alai Mountain system, particularly in the Zarafshan and Hissar Ranges, and in areas around the Fergana Valley. In Uzbekistan, *Malus sieversii* is concentrated in the western part of Tian Shan Mountains, particularly in the Chatkal Range, the Ugam Range, and the western slopes of the Kuramin Range (**Figure 1**) [11].

The wide spread and adaptability of *Malus sieversii* emphasize its importance in both natural ecosystems and agricultural research. Developing an understanding of these particular adaptations of apple cultivars can offer valuable insights into the development of resilient apple varieties that can thrive in a wide range of environmental conditions.

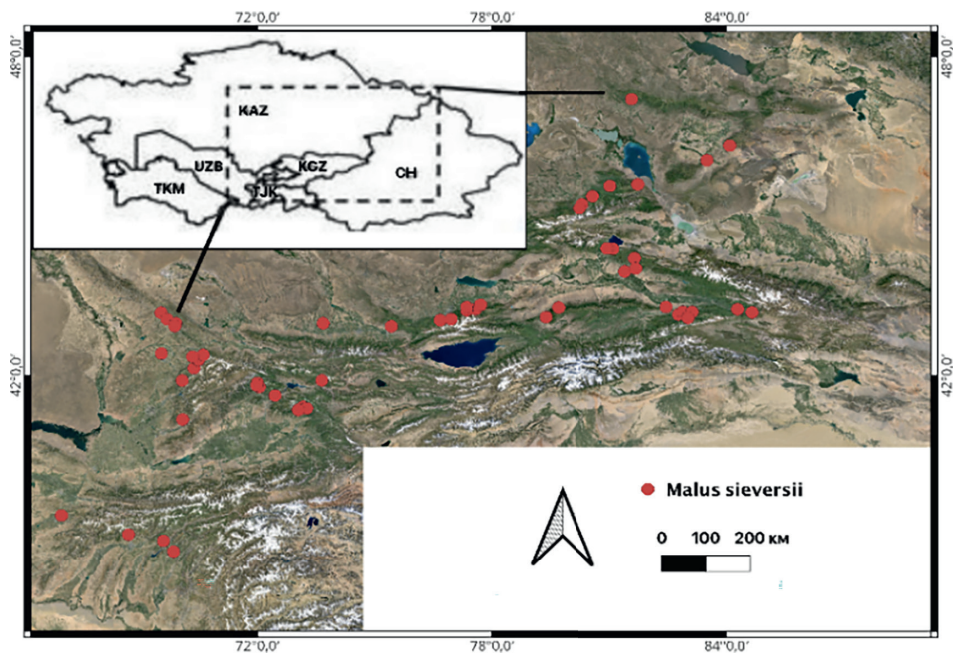


Figure 1.
Distribution of *Malus Sieversii* in Central Asia and China.

2.2 Genetic diversity and contributions to modern apples

In 2010, scientists sequenced the complete apple genome to gain a better understanding of the genesis and evolution of apples. Comparative investigations indicated that *M. domestica* cultivars exhibited a closer genetic relationship with the wild species *M. sieversii*, rather than *Malus sylvestris* and *Malus orientalis* [1]. The domestication of apples (*Malus domestica*) began 4000 and 10,000 years ago with the selection of *Malus sieversii* from Central Asia, for desirable traits. This process was further enhanced by hybridization with other wild species like *Malus sylvestris*, *Malus orientalis*, and *Malus baccata* introducing new genetic diversity [12–14]. The development of grafting techniques allowed for the propagation of elite cultivars, facilitating the spread of desirable apple varieties. As apple cultivation spread across different regions, local preferences and environmental conditions led to a diverse array of apple cultivars, each adapted to specific climates and tastes. The Silk Road was instrumental in this process, acting as an extensive network of trade routes that connected the East and West, facilitating the exchange of goods, culture, and agricultural practices, thereby enhancing the genetic diversity and adaptability of cultivated apples.

Malus sieversii exhibits an extensive range of morphological characteristics, particularly in its fruits and pollen grains, and possesses significant genetic and phenotypic variation. Morphologically, it closely resembles the cultivated apple tree (*Malus domestica*). The height of the wild apple tree, *Malus sieversii*, varies between 2 and 12 meters, with a few specimens growing reaching as high as 14 meters, with a gray-brown or dark gray trunk and a broad crown. The branches are thick, sometimes with thorns (on young shoots). The one-year-old shoots are short, greenish-brown or brown, pubescent, while the two-year-old shoots are dark gray or gray. The leaves are large, measuring 6–11 cm in length and 3–5.5 cm in width, broadly lanceolate or

oblong-elliptical, with a wedge-shaped base, ranging from serrate-dentate to serrate. They are dense, usually glabrous on the upper side, and more or less felted hairy on the underside. The petioles are rather thick and felted hairy. The tree begins to bear fruit at around 12 years of age. The seeds of *Malus sieversii* are wedge-shaped or oval, appearing grayish or brownish-brown when dry; dull and smooth, with a length of 5–6 mm and a width of 3–4 mm. The inflorescence consists of 3–5 flowers. The flowers are large, with a diameter of 3.5–6 cm, and are pale pink or white. The hypanthium is felted pubescent. The fruits of this apple species vary in shape, being distinctly round, flattened-round, rounded conical, elongated round shape, and greater in size compared to other wild apple species. On average, their diameter ranges from 3 to 4 cm, occasionally reaching up to 7 cm. The skin of the fruit can be colored in various shades, including green, yellow, and red, depending on the degree of ripeness and growing conditions. The pulp of the fruit is juicy, with a characteristic sweet and sour, sometimes bitter-sweet taste. The flowering period typically occurs between April and May, while the fruit ripening from August to September. The average age of apple trees is 50 years. Under optimal circumstances, its lifespan can reach a maximum of 150 years [15–17].

In addition to its diverse morphological traits, *Malus sieversii* demonstrates remarkable resistance to various environmental stresses. It exhibits high tolerance to cold, drought, and diseases. Its cold resistance allows it to thrive in harsh climates, while its drought resistance enables survival in arid conditions. Furthermore, *Malus sieversii* has shown resistance to several common apple diseases, including apple scab, fire blight, and powdery mildew. Consequently, *Malus sieversii* has significantly contributed to the genetic makeup and phenotypic traits of *Malus domestica*, particularly in terms of fruit quality, pathogen resistance, and genetic diversity. These contributions have played a crucial role in the domestication and improvement of cultivated apples.

Genetic diversity studies of *Malus sieversii* have been essential for grasping its potential for apple breeding and conservation. The wild apple specimens collected by the USDA-ARS Division of Plant Genetic Resources in Geneva, New York, USA, during expeditions to Central Asia, have been the focus of extensive research on genetic diversity. Researchers have utilized different molecular markers, including SSR (simple sequence repeat) and SNP (single nucleotide polymorphism) markers, to examine the genetic diversity within and among populations of *Malus sieversii*. These studies have uncovered a significant degree of genetic variability, which is crucial for the species' ability to adapt and withstand changes in the environment. Lamboy et al.'s study on the allozyme diversity revealed that *Malus sieversii* has high genetic diversity, surpassing other *Malus* species, and despite some geographic differentiation, there is significant genetic mixing [18]. Geibel et al. noted significant disease resistance in wild apple trees, with some accessions showing complete absence of apple scab (*Venturia inaequalis*) and powdery mildew (*Podosphaera leucotricha*). Pre-selected resistant individuals did not show the presence of the scab resistance-associated Vf gene in a study using molecular markers, such as Sequence Characterized Amplified Region (SCAR) and random amplified polymorphic DNA (RAPD), suggesting the potential existence of new resistance genes in these populations [19]. In the study conducted by Forsline et al., seedlings from Kazakhstan (Karatau and Tarbagatai regions) exhibited variations in their resistance to apple scab, rates of natural infection by fire blight in Tarbagatai region, and varied fruit characteristics and highlighted their importance as a valuable resource for apple breeding programs that aim to enhance disease resistance and horticultural traits [20].

The study using microsatellite markers showed high genetic diversity and significant differentiation among populations of *Malus sieversii* in Kazakhstan. Genetic differentiation corresponded with geographical locations, with more admixture observed in the southwestern populations [21]. In the same year, the authors successfully identified a subset of 35 *Malus sieversii* individuals that complements existing core subsets by representing all major genetic lineages and capturing significant genetic and phenotypic diversity, thus aiding in the long-term conservation and utilization of these genetic resources for breeding and research purposes [22]. The research by Volk et al. revealed that the *M. sieversii* collection in the NPGS exhibits diverse genotypic and phenotypic traits, including highly overlapping gene pools within related taxa *Malus pumila*, *Malus pumila* var. *niedzwetzkyana*, *M. sieversii* var. *kirghisorum*, and *M. sieversii* var. *turkmenorum* [23]. Recent studies highlighted the prevalent crop-to-wild gene flow of apples in Kazakhstan, posing an accelerated risk of genetic swamping [24, 25].

The study conducted by Tao et al. on the wild apples from different sites of the Ily state in China demonstrated great variation in fruit shape, size, color, and length. The study also found significant genetic variations in mineral elements' content in ripe fruits, suggesting potential for further selection [26]. The study of genetic diversity in Xinjiang, China, using SSR markers revealed the highest genetic diversity and high gene flow between populations, indicating some degree of gene exchange [27]. *Malus sieversii* exhibited resistance to Valsa canker, a disease caused by the fungal fungus *Valsa mali*. Studies have identified particular transcription factors, including MsbHLH41 and MsEIL3, which have significant functions in the plant's defense systems against this pathogen [28].

Genetic diversity studies have continued to underline the critical importance of *Malus sieversii* in the improvement and sustainability of modern apple cultivars. As existing research leads to new discoveries about resistance genes and beneficial traits, conservation of *Malus sieversii* continues to be relevant for making these apple varieties adaptable and resilient in the future.

3. Conservation, challenges, and future prospects

3.1 Current status and threats to wild populations

Despite its historical and genetic importance, *Malus sieversii* faces numerous conservation challenges. The loss of natural habitats, the impact of climate change, and human activities have resulted in a decrease in wild populations, posing a threat to genetic variety [29, 30]. This genetic diversity is essential for future breeding efforts. Conservation actions are crucial for preserving this species and its genetic resources. Diverse strategies, including the establishment of protected areas, *in situ* and *ex situ* conservation projects, and international collaboration, are implemented to save *Malus sieversii*. In 2007, *Malus sieversii* was evaluated for the IUCN Red List of Threatened Species and classified as vulnerable species [31]. It is listed in the Red Books of Kazakhstan, Kyrgyzstan, and China [32]. There are several genetic reserves in Kazakhstan for the conservation of Sievers apple trees. These reserves are mainly located on the territory of the Ile-Alatau and Dzungarian-Alatau national parks and 75% of the wild apple trees of Kazakhstan are distributed in these regions (Figure 2). The total area of orchards with wild Sievers apple trees in Kazakhstan, according to 2012 data, was about 14,307 hectares [33].



Figure 2.
Malus sieversii in the ripening season. A - *Malus sieversii* from Ile Alatau Natural Park, B - *Malus sieversii* from Zhongar Alatau National Park.

The decline of wild apple habitats in Kazakhstan began in the 1950s, during the Soviet era, when a large-scale process of replacing wild apple trees with cultivated varieties and creating terraced gardens on mountain slopes was carried out [34]. As a result, hundreds of hectares of apple trees were uprooted. In addition, urbanization near the metropolis of Almaty in the southeast of the country, where the Ile-Alatau State National Nature Park is located, also had an impact. This also likely facilitated gene flow from cultivated to wild varieties, as the proximity of cultivated apple trees to wild apple populations increased the chances of cross-pollination. Gene flow has the potential to bring novel genetic material into wild populations, potentially modifying their genetic composition and impacting their capacity to respond to natural environmental fluctuations. This genetic exchange may also have an effect on the total biodiversity of a region, resulting in alterations to the distinctive traits of wild apple populations. Over the past 50 years, the extent of fruit forests in the Ile-Alatau region has declined by 30%, and in certain areas, the decline has been as high as 70%. The apple forest area in the Maly Almaty Gorge was 190 hectares in 1934, but decreased to only 9 hectares in 2004, 70 years later. In the Dzungarian Alatau, the area of apple forests has decreased by 28% since 1960 [35, 36]. The Dzungarian Alatau, due to its isolation, has been less exposed to anthropogenic impact, which has contributed to the preservation of significant genetic diversity of the wild apple. However, the region is still subject to the influence of insect pests, abiotic factors, and natural aging of trees, which threatens the sustainability of populations (**Figure 2B**).

The wild apple trees in Kazakhstan are affected by the spread of various insect pests, such as the apple ermine moth (*Yponomeuta malinellus* Zell), hawthorn leaf roller (*Cnephasia crataegana* Hb.), spongy moth (*Lymantria dispar*), codling moth (*Cydia pomonella*), aphids (*Aphidoidea*), and the San Jose scale (*Quadraspidotus perniciosus*) [37]. These pests cause damage on the fruits, leaves, shoots, bark, and wood of the trees, leading to a weakening of the plants and a decrease in their productivity.

In 1999–2003, the apple ermine moth (*Yponomeuta malinellus* Zell) caused significant devastation to the apple thickets in the Dzungarian Alatau, resulting in approximately one-third of the trees turning into dead wood. Subsequently, this dangerous pest also appeared in the Ile-Alatau, further threatening the apple populations in that region [34].

Additionally, while some wild apple trees exhibit resistance to various diseases, others remain susceptible to infections, such as apple scab (*Venturia inaequalis*), powdery mildew (*Podosphaera leucotricha*), fire blight (*Erwinia amylovora*), and phytophthora root rot (*Phytophthora* spp.) [38].

In China, the wild apple is significantly threatened by the wood-boring beetle (*Agrilus mali*), which damages the tree's vascular system, and the fungal pathogen *Valsa ceratosperma* (or *Valsa mali*), which causes cankers on branches and trunks that can lead to tree death [39, 40].

3.2 Conservation efforts and their importance

The conservation of wild apple species is crucial for preserving biodiversity and ensuring the long-term viability and progress of cultivated apple varieties. It is also essential for the sustainability of apple agriculture, particularly for future breeding programs on a worldwide basis. The genetic variety present in populations of *Malus sieversii* is a valuable resource for breeders and researchers, offering a collection of genes that can be utilized to enhance disease resistance, climate adaption, and overall strength of cultivated apple varieties. The genetic reservoir plays a crucial role in the context of climate change, since it provides a valuable resource for developing crop varieties that can withstand new challenges faced by the environment.

However, the main conservation challenges encountering *Malus sieversii* involve substantial habitat degradation resulting from agricultural expansion and urbanization, predicted complete habitat loss due to climate change in regions, such as Zhambyl of Kazakhstan, Tajikistan, and Uzbekistan, and fragmented populations impeding genetic interchange. Insufficient protected areas do not effectively protect appropriate habitats, and land use changes disproportionately impact environmental factors, such as elevation and soil pH. To effectively maintain *Malus sieversii*, conservation planning requires dynamic prioritizing, with a focus on long-term monitoring and adaptive management measures [32].

The process of grafting trees from a natural population with varietal material and cultivating gardens on its lands, which was prevalent in the mid-twentieth century in Kazakhstan, results in alterations to the genetic composition. These changes decrease the ability of a natural population to survive, and the most crucial strategies to protect them involve restoring the original population structure. To begin, it is crucial to prevent the cross-pollination of wild plants with cultivated types and partially cultivated trees. It is important to remove trees exhibiting evidence of varietal DNA and establish buffer zones of two kilometers surrounding natural populations. Within these buffer zones, the growing of both varietal and “semi-cultivated” apple materials should be prohibited. Regular monitoring of the condition of indigenous apple populations is crucial [41].

In situ conservation, which involves protecting *Malus sieversii* in its original habitat, is of the greatest significance. It is crucial to make efforts to save these habitats from deforestation, urbanization, and agricultural encroachment. National parks

and genetic reserves are crucial components of this strategy. Academician Aimak Dzhangaliev created several selection and genetic reserves of Sievers apple trees in the territory of Kazakhstan and developed 27 elite varieties-clones of apple trees. Currently, several genetic reserves are experiencing a decrease in vegetation caused by both biotic and abiotic factors, as well as the degradation and aging of the population, this population decline is a significant factor contributing to the extinction of major wild plant species. There are a significant number of old trees in the Zhongar Alatau State National Nature Park (**Figure 3**). To address the degradation of old trees and the overall decline in vegetation, it is essential to implement restoration programs and create new, modern genetic reserves. Restoration involves not only planting new trees but also ensuring that these trees are genetically diverse and resilient.

Ex situ conservation efforts complement *in situ* strategies by preserving genetic material outside of its natural habitat. Botanical gardens, seed banks, and research institutions around the world are actively involved in collecting and maintaining *Malus sieversii* germplasm. These collections serve as genetic libraries that can be accessed for research and breeding purposes. The USDA National Plant Germplasm System (NPGS) and The Main Botanical Garden of Kazakhstan are notable examples of such repositories. These institutions ensure that even if natural populations are lost, the genetic heritage of *Malus sieversii* will be preserved.

Conservation efforts for *Malus sieversii* are vital to maintaining the genetic basis of domesticated apples and ensuring the sustainability of future apple crops. Protecting this species requires a multifaceted approach combining *in situ* and *ex situ* strategies, international cooperation, political support, and community engagement. Continued commitment to the conservation of *Malus sieversii* will not only preserve a key genetic resource but will also contribute to global food security and agricultural sustainability.



Figure 3.
Multispectral imaging of the Malus sieversii population from a genetic reserve in Zhongar Alatau State National Nature Park.

4. Conclusion

This chapter explores the historical discovery of *Malus sieversii*, its genetic contributions, and the ecological adaptations that have shaped the physical characteristics of domesticated apples. It also delves into current conservation issues and efforts, emphasizing the importance of preserving *Malus sieversii* for future breeding and research programs. By understanding the role of this wild ancestor, we can better appreciate the diversity and resilience of contemporary apple varieties and work toward sustainable and innovative apple cultivation practices.

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