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# Aronia mitschurinii: Solving a Horticultural Enigma

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*Aronia mitschurinii*: Solving a Horticultural Enigma

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*Aronia mitschurinii*: Solving a Horticultural Enigma

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## Abstract

*Aronia* (Medik.), commonly known as chokeberry, is a taxonomically misunderstood genus currently experiencing a renaissance in North America as both an ornamental and fruit crop. It serves as an alternative for non-native, invasive ornamental species and has been discovered to be a rich source of antioxidants. Three species of chokeberry are commonly accepted as native in North America: *A. arbutifolia* (L.) Pers. red chokeberry; *A. melanocarpa* (Michx.) Elliot, black chokeberry; and *A. prunifolia* (Marshall) Rehder, or purple chokeberry.

In Europe a fourth species of human origin is recognized as *Aronia mitschurinii* (A.K.Skvortsov & Maitul.), or cultivated, black-fruited *Aronia*. In North America this type of *Aronia* is described as cultivars of *A. melanocarpa*. ‘Viking’, ‘Nero’, and ‘Aron’ are the most notable cultivars that could be considered *A. mitschurinii*, however, these cultivars are virtually indistinguishable from one another. This species (or cultivar) is characterized by near homogeneity of the population, tetraploidy, and a distinct morphology with more robust stems, wider leaf blades and larger fruits than wild populations of *A. melanocarpa*. It is widely speculated that this genotype originated in the early 20<sup>th</sup> century with Russian pomologist Ivan Michurin, as the product of his experiments in wide hybridizations. In my research I attempt to determine the feasibility of this hypothesis by exploring *Aronia*’s crossing capabilities and testing the relationships of *A. mitschurinii* to wild *Aronia* species and several other Pyrinae genera using amplified fragment length polymorphic (AFLP) analysis. AFLP binary data was interpreted by the NTSYSpc software package into a similarity matrix using Jaccard’s

coefficient. Data was also interpreted by the Structure 2.3.3 software package using Bayesian statistical method.

Results from the hybridizations indicate tetraploid *Aronia* produces seed apogamously and cannot be used as a maternal parent in crosses. Diploid *Aronia melanocarpa* produces seed amphimictically and can be utilized as a maternal parent. Successful seed formation was achieved between maternal diploid *A. melanocarpa* and *Malus domestica*, *Photinia serrulata*, *Sorbus*, and  $\times$ *Sorbaronia*.

Clustering of AFLP similarity data using the unweighted pair group method with arithmetic mean (UPGMA) identified *A. mitschurinii* as distinct from wild *Aronia* spp., placing it on a branch with  $\times$ *Sorbaronia fallax* and  $\times$ *Sorbaronia* 'Ivan's Beauty'. Non-metric multidimensional scaling (nMDS) clustered *A. mitschurinii* apart from wild *Aronia* spp., and demonstrated a relationship between *Sorbus aucuparia*,  $\times$ *Sorbaronia fallax*, and *Aronia*. Bayesian analysis revealed *A. mitschurinii* to possess genetic influence from the genus *Sorbus* subgenus *Sorbus*.

It is hoped that this data can identify potential avenues for further germplasm improvements and aid in the development of novel *Aronia* varieties.



## **Chapter I**

### **An Introduction to the Genus *Aronia*; *Aronia mitschurinii*: Historical Commercial Cultivation and Future Potential**

## Introduction

*Aronia* (Medik.), or chokeberry, is a group of deciduous, multi-stemmed, rosaceous shrubs native to eastern North America. Members of the genus are highly adaptable, rhizomatous, opportunistic species that have significant potential as both ornamentals and fruit crops (Brand, 2010). Hardin (1940), Graves (1956) and Krussmann (1986) characterized the genus by its simple, alternately arranged leaves with dark glands on upper midribs of leaf blades; appressed buds with five outer scales; bundle scars in 3s; small stipules that abscise; corymb inflorescence with white to pale pink, spreading five-petaled flowers connately lobed; numerous stamens, purple anthers; inferior, five celled ovary, five pistils connate at base with free styles; and pome fruits. Species boundaries are poorly defined in *Aronia* due to apogamy, hybridization, and polyploidy, however three species are recognized by a majority of authorities.

Red chokeberries (*A. arbutifolia* (L.) Persoon) are typically characterized by red fruits and pubescence on the leaves (Rehder, 1940; Graves, 1956; Hardin, 1973; Dirr, 2009; Brand, 2010). *Aronia arbutifolia* is a more southern species than black chokeberry (*A. melanocarpa* (Michaux.) Elliot) and can be found along the Atlantic plain ranging into Northern Florida and west to Texas (Rehder, 1940; Graves, 1956; Hardin, 1973; Rossell and Kesgen, 2003; Weakley, 2007; Dirr, 2009; Brand, 2010). Considered hardy to zone (3)4 (Dirr, 2009) or zone 5 (Rehder, 1940; Krussmann, 1986), records of plants at higher latitudes are likely misidentified *A. prunifolia* (Marshall) Rehder .

Black chokeberry is generally accepted as a more cold hardy species than the red, with cold hardiness reported to either zone 4 (Rehder, 1940) or zone 3

(Krussmann, 1986). *Aronia melanocarpa* naturally comprises the northern range of the genus and is found from the Maritimes in Canada west into the upper Mississippi Valley and south along the Appalachian mountains (Rehder, 1940; Graves, 1956; Hardin, 1973; Rossell and Kesgen, 2003; Weakley, 2007; Dirr, 2009; Brand, 2010). This species is typically the smallest of the three in habit and can be found in both dry and wet sites.

The third species is *A. prunifolia* or purple chokeberry. This type of chokeberry is more ambiguous, since it shares both range and morphology with the black and red species (Hardin, 1973). It is likely an interspecific hybrid between black and red chokeberry with phenotypes closely resembling either of the parents (Dirr, 2009). Fruits are often the most reliable identification feature (Hardin, 1973), typically purple-black to dark purple (Rehder, 1940). A detailed description of individual *Aronia* species, their morphology and commercial uses is described later in this chapter.

## **I. Taxonomy**

### *The apple subtribe*

*Aronia* falls within the subtribe Pyrinae (Rosaceae), formerly known as the Maloideae, or colloquially as the apple subtribe (Potter et al., 2007). Presently this taxonomic group consists of approximately 950 species and 30 genera including many important food sources such as *Malus*, *Pyrus*, and *Eriobotrya* (loquat), as well as ornamentals like *Chaenomeles*, *Cotoneaster*, *Photinia*, and *Sorbus* (Evans and Campbell, 2002; Campbell et al., 2007). The group is monophyletic based on its unique fruit, a pome, and was first outlined as twelve genera by Lindley (1822) as Pomaceae (Robertson et al., 1991). The earliest treatment for an *Aronia* species, *Mespilus*

*arbutifolia*, described by Carl Linnaeus in 1753, was among the original founding genera. Early authorities, including Filius Linnaeus and French botanist Jean de Lamarck, included *Mespilus arbutifolia* in either *Pyrus* or *Crataegus* (Linnaeus, 1782; Lamarck, 1783) leading to *Aronia* synonyms in both genera (Table 1). Medikus (1789) and Persoon (1806) were the first accepted naming authorities to use the name *Aronia*. German botanist Gustav Heinhold (1841) placed *Aronia* within *Sorbus*, a treatment that has persisted into the 20<sup>th</sup> century. Sax (1931) argued for this based on the propensity for hybridization between the two genera. More recently, Robertson et al. (1991), placed *Aronia* within *Photinia* based on floral and fruit structure. Using sequence data, Campbell et al. (2007) did not find support for this and kept *Aronia* as a standalone genus. However, most relationships within the Pyrinae remain unresolved.

Pyrinae is not only unique within Rosaceae for its pome fruits, but also for its base chromosome count of 17. Many competing theories about the origin of this group have been proposed. The first was developed by Nebel (1929) and referred to as the rosoid hypothesis (Evans and Campbell, 2002). This theory suggests an autopolyploidization event involving a Rosoid ancestor, increased the base chromosome count from seven to 35. This was followed by an aneuploid loss of one chromosome and a haploid event, leaving a base count of  $x=17$ . Darlington and Moffett (1930) supported autopolyploidization as a method of creation for the Pyrinae based on observations of multivalent chromosomes.

A competing theory to the rosoid hypothesis is the wide-hybridization, or allopolyploid hypothesis developed by Karl Sax (1931, 1932, and 1933). The theory states that the Pyrinae was the product of an ancient hybridization between Rosaceous

Amygdaloideae (a now delimited clade containing *Prunus*) with a base chromosome count of  $x = 8$ , and the Spiraeoideae with a count of  $x = 9$ . Sax based his hypothesis primarily on the obvious simplicity and propensity for wide hybridizations within the group. He also noticed numbers of univalent chromosomes in triploid hybrids during meiosis, going so far as saying there was a cytological basis for inclusion of the entire group within a single genus. Sax's theory (though not his broad generic inclusion) was later supported by isozyme studies (Chevreau et al., 1985) and fruit morphology (Stebbins, 1950; Phipps et al., 1991).

The currently accepted theory regarding the origin of the Pyrinae proposes it originated from an autotetraploid event, not an autopentaploidization as proposed by Nebel (1929) and Darlington and Moffett (1930), or a wide hybridization as proposed Sax (1931, 1932, and 1933). Overlooked by the previous two theories is the presence of traditional Spiraeoid genera, *Gillenia*. This genus possess floral and fruit morphology similar to Pyrinae (Sterling, 1966; Morgan et al., 1994; Campbell et al., 1995 and Evans, 1999) and a chromosome count of  $x=9$  (Goldblatt, 1976). The autopolyploid hypothesis is based on the work of Goldblatt (1976), Morgan et al. (1994), Campbell et al. (1995), Evans (1999), Evans et al. (2000, 2002) and Potter et al. (2002, 2007). These studies also support the theory that the subtribe is of American origin as *Gillenia*, *Vauquelinia* and *Lindleya* are only found in the New World. Fossil records indicate speciation commenced approximately 50 million years ago, almost 80 million years after formation of the Atlantic rift (Wolfe and Wehr, 1988).

## II. *Aronia*

### *Aronia arbutifolia*

Red chokeberry is reasonably easy to distinguish from black chokeberry, however, purple chokeberry types often share morphology with both red and black chokeberry, making them extremely difficult to differentiate (Hardin, 1973). The most notable feature of *A. arbutifolia* is its bright red fruits, 5-7 mm in diameter, ripening late September to October (Rehder, 1940; Hardin, 1973; Brand, 2010). Plants with fruits that mature red-brown, ripen earlier than October and are found in New England, are likely *A. prunifolia*. Red chokeberry fruits have been described as persisting into and even through the winter (Rehder, 1940; Hardin, 1973; Dirr, 2009), but in areas outside its natural range fruit may also desiccate and fall off in late autumn.

A second distinguishing feature of *A. arbutifolia* is the presence of tomentum on the underside of leaf blades, and on the surfaces of first year twigs, rachis and pedicels (Rehder, 1940; Hardin, 1973; Krussmann, 1986; Dirr, 2009; Brand, 2010). Though red chokeberry shares this feature with many types of purple chokeberry, pubescence is typically denser on the red species and very distinct from *A. melanocarpa*. However, individual trichomes on all three species appear identical (Hardin, 1973). Leaves of *A. arbutifolia* are elliptic to oblong or obovate, 4-8 cm long, acute to acuminate, serration is fine with black-tipped teeth (Rehder, 1940; Graves, 1956; Hardin, 1973; Krussmann, 1986; Dirr 2009). Hardin (1973) indicates the bright red fall color is fairly uniform for the species and a good identification feature. The cultivar ‘Brilliantissima’ is lauded by Dirr (2009) as a “superior” form and a suitable replacement for winged *Euonymus* (*Euonymus alatus*) due to its glossy, red fall foliage.

Mature habit of the plant is another somewhat distinctive characteristic of red chokeberry. *Aronia arbutifolia* is typically considered more upright than the black, reaching heights of 3 m or more (Rehder, 1940; Dirr, 2009; Brand, 2010). Smaller individuals of 1.5-2 m (Krusmann, 1984) are likely immature specimens, misidentified or responding to environmental factors. Mature individuals often lack foliage on lower portions of the plant and appear leggy (Dirr, 2009; Brand, 2010).

*Aronia arbutifolia* is biologically centered in the southeastern Atlantic coastal plain of the United States and into northern Florida. It can typically be found growing in moist areas such as fens, swamps, savannahs, creek and lake banks, moist rocky ledges and damp pine-barrens (Hardin, 1973; Rossell and Kesgen, 2003; Weakley, 2007; Brand, 2010). The exact extent of its range is somewhat ambiguous. Graves (1956), Hardin (1973), and Weakley (2007) place its northern range as the provinces of New Brunswick and Nova Scotia, Canada. Others are less supportive of distribution north of southern New England, placing its northern limit in coastal Massachusetts (Rehder, 1940; Dirr, 2009; Brand, 2010). Few sources list a specific western boundary. Dirr (2009) accepts Rehder's (1940) limit as the Mississippi river basin from Minnesota to Texas. The *Aronia* collection at the University of Connecticut includes a red chokeberry individual from eastern Texas, but none of the plants collected from the upper Midwest have proven to be *A. arbutifolia*. Most authorities list Appalachian Kentucky and West Virginia as the northwestern boundary for *A. arbutifolia* (Graves, 1956; Hardin, 1973; Krusmann, 1986; Rossell and Kesgen, 2003; Weakley, 2007; Brand, 2010). The hesitancy of many authors to list a definitive range for *A. arbutifolia* likely reflects identification confusion with *A. prunifolia*, especially in northern latitudes.

*Aronia arbutifolia*'s ornamental value lies with its small white flowers, born on cymes of 9-20 (Dirr, 2009) in early to mid-May (Brand, 2010) they are mildly fragrant and contrast with dark green foliage. Though a wetland native, Dirr (2009) highlights its adaptability in the landscape and observations of specimens growing on the University of Connecticut Storrs campus reinforce its ability to handle exposed, dry conditions. Red fall color is superb and the addition of glossy red fruits adds to its appeal.

A problem for tetraploid chokeberry is a lack of genetic diversity (Persson-Hovmalm et al., 2004). Genetic introgression for *A. arbutifolia* is unlikely as the species appears to be uniformly tetraploid (Moffett, 1931; Brand, 2010), though Sax (1931) lists it as a diploid. Unfortunately, Sax does not reference the source of plants used in his analysis. Hardin (1973) determined this species to have a short, unspecific protogyny and exhibit a high degree of autogamy or apogamy. Apomixis is common within the Rosaceae and well documented in related *Amelanchier* (Campbell and Wright, 1996 and Campbell et al., 1999).

### *Aronia melanocarpa*

*Aronia melanocarpa* is most easily identified in the mid- to late summer by the presence of black fruits. The exact color of fruits can be pure black (Hardin, 1973; Krussmann, 1986; Brand, 2010) or purplish black (Rehder, 1940; Graves, 1956; Dirr, 2009). Pomes are typically larger, 8-10 mm, than for red chokeberry. They are glossy and ripen from July-September (Hardin, 1973; Krussmann, 1986; Brand, 2010).

Leaves can be useful for identification when fruits are not present. *Aronia melanocarpa* is typically described as having completely (Graves, 1956; Dirr, 2009;



Brand, 2010) or nearly glabrous foliage and stems (Rehder, 1940; Krussmann, 1986) in contrast to the pubescent red and purple species. Blades are 2-4 cm long, elliptic or obovate to oblong-ob lanceolate, abruptly acuminate or obtusish, finely serrate and exhibiting a deep glossy green top that is somewhat lighter beneath (Rehder, 1940; Krussmann, 1986; Dirr, 2009). Serration is sometimes used as a diagnostic feature as the black species often lacks *A. arbutifolia*'s distinctive black glands on the teeth, although Hardin (1973) argues against this citing too much heterogeneity. Fall color of black chokeberry is much more variable than the red species. Dirr (2009) describes it as wine-red, Brand (2010) as yellow to orange-red. The cultivars 'Morton' (Iroquois Beauty™) and 'McKenzie' were noted by Dirr (2009) for superior form and foliage. Hardin (1973) indicates red fall foliage color is distinct to *A. arbutifolia*, implying that plants of *A. melanocarpa* exhibiting red fall foliage must be *A. prunifolia*.

Habit can be a helpful distinguishing feature of *A. melanocarpa*. While red chokeberry tends to grow more upright, black chokeberry is typically described as a low shrub of 1 m (Rehder, 1940; Krussmann, 1986) to 2.4 m (Dirr, 2009; Brand, 2010). Once again, habit can vary based on cultural factors and specific genotype. The overall shape of plants is more uniform and less leggy than described for *A. arbutifolia*, with foliage persisting along stems nearly to the ground on most specimens.

Habitat and distribution is somewhat ambiguous for the same reasons listed for *A. arbutifolia*, most notably its confusion with *A. prunifolia*. It is generally accepted that black chokeberry can be found as far north as Newfoundland and into the Great Lakes region (Hardin, 1973; Brand, 2010). Most sources agree it is found throughout the Appalachian Mountains into Georgia. Brand (2010) and Persson-Hovmalm et al. (2004)

indicate New England populations are typically diploid implying the region is likely the species center of biodiversity. Plants can be found growing in wet areas described for *A. arbutifolia*, but they are also commonly found colonizing dry dunes and rocky slopes (Hardin, 1973, Rossell and Kesgen, 2003; Weakley, 2007; Brand, 2010) and commonly cohabitates with lowbush blueberry (*Vaccinium angustifolium*) (Hall et al., 1978; Yarborough, 1985).

### *Aronia prunifolia*

Purple chokeberry is the most problematic of *Aronia* species to characterize, however, most authorities acknowledge it as an intermediate species between *A. arbutifolia* and *A. melanocarpa*. It is most often described as similar to *A. arbutifolia* in appearance (Rehder, 1940; Krussmann, 1986; Dirr, 2009). Rehder (1940) describes *A. prunifolia* as possessing purplish black fruits, heights up to 4 m, looser, less pubescent (than *A. arbutifolia*) inflorescences, and lustrous 8-10 mm diameter fruits. Krussmann (1986) concurs with this description and indicates that *A. prunifolia* habit parallels that of *A. arbutifolia*. Hardin (1973) acknowledges *A. prunifolia*, but considers it to exhibit too many phenotypes to be formally recognized describing it broadly as having morphology intermediate between the red and black species with somewhat persistent purplish black fruits, pubescent leaves and branches that become increasingly glabrous as they mature. Harden describes the range for *A. prunifolia* as overlapping the range of both black and red chokeberry, especially along the Appalachians. It is the opinion of colleagues Connolly and Brand (unpublished data) that most plants classified as red chokeberry in

New England are actually misidentified individuals of *A. prunifolia*, having been observed prior to fruit ripening.

The fact that *A. prunifolia* has so many intermediate features between *A. arbutifolia* and *A. melanocarpa* suggests that it is an interspecific hybrid. Rehder (1920) distinguishes *A. prunifolia*, the wild form found in North America, from *A. floribunda* (Lind) Spach., a garden hybrid originating in Europe. Hardin (1973), however, considers these one and the same. He presents the theory that purple forms are hybrids either from ancient events, or recent crosses, citing overlapping ranges and no biological barriers (except apomixes). Brand (2010) noted that *A. melanocarpa* and *A. arbutifolia* can be easily crossed and determined that wild collected *A. prunifolia* are polyploids. Agamic seed production appears to be prevalent in this species and could explain how the hybrid species can be stable and self sustaining. Accepting *A. prunifolia* as a distinct hybrid species then raises the question of whether a hybrid “x” designator should be used with the name. Dirr (2009) uses this terminology, however Rehder (1938 and 1940) does not. The use of the “x” designator denotes a controlled cross and documented lineage (Dirr, 2009). Since there were likely multiple crosses at various points throughout history it is appropriate to omit the designator.

### **III. *Aronia mitschurinii***

*Aronia mitschurinii* (Figure 1), or cultivated black-fruited *Aronia*, was first proposed by Skvortsov and Maitulina (1982) distinguishing it from its North American relatives. The species developed in early 20<sup>th</sup> century Russia, most closely resembles *A.*

*melanocarpa*, but possesses some distinct differences. Skvortsov and Maitulina (1982) characterized *A. mitschurinii* by near complete homogeneity of the population, rounder leaves (Figure 2), globular fruits with masses 2-3 times that of wild *A. melanocarpa* (Figure 3), larger, more numerous flowers, zone 2 cold hardiness and tetraploidy. Kask (1987) listed the mature height at 3 m. Observations of *A. mitschurinii* growing alongside wild *A. melanocarpa* in Connecticut reveal its superior vigor, coarser branching structure and wider leaf blades. Plants were observed to reach approximately 2 m after 4 years. Commercial propagation is predominantly by seed (Kask, 1987) with plants suspected of apogamy (Skvortsov and Maitulina, 1982 and Persson Hovmalm et al., 2004). Grown as an orchard crop primarily for juice, cultivation in the Soviet Union reached a peak production of 17,800 ha by 1984 (Kask, 1987).

#### *European breeding and cultivation*

The species Skvortsov and Maitulina (1982) describe as *A. mitschurinii* is synonymous with the *A. melanocarpa* cultivars ‘Viking’, ‘Nero’ and ‘Aron’, however current research indicates they belong to a single genotype (Persson-Hovmalm et al., 2004). The first reports of black-fruited *Aronia* in eastern Europe are cited by Skvortsov et al. (1983) as in the town of Kremenets, Ukraine, in 1816 and in collections at Kharkiv University in 1823. Specimens from this period appeared morphologically similar to wild North American *A. melanocarpa*. Additional sources cited by Skvortsov et al. (1983) list it grown solely as an ornamental prior to the 20<sup>th</sup> century. It was not until the first decades of the 1900s, after Ivan Michurin (1855-1935) began working with *Aronia*, that the first reports of new forms began to emerge in Europe.

Michurin describes his first cross in 1905 with Chernoplodnaya mountain-ash (*Sorbus melanocarpa* Neynh.) that he received from Germany. This excerpt is from Michurin's notes compiled after the researchers death (Michurin, 1948):

"In order to produce new varieties of sweet mountain ashes and promote them in northern regions and Siberia, I hybridized in 1905 our inedible mountain-ash *S. aucuparia* with a mountain-ash *Sorbus melanocarpa* Neynhold, which I obtained from Germany and which has sweetish, edible fruits. I named the resulting "Likernaya". It is completely hardy in our harsh winter weather. The fruit of the new cultivar is completely black, sweet, good for preserves [and] alcoholic beverages."

Michurin's notes also describe *S. melanocarpa* as possessing a low bushy crown, closely spaced branches and black fruits suitable for preserves and jams. He indicates this genotype will "acquire great importance in our hybridization work." Michurin subsequently crosses 'Likernaya' with *Mespilus germanica* in 1926 producing what was called 'Michurin's Dessert' or 'Dessertnaya'. Michurin considered 'Dessertnaya' the best of his hybrids up until that point. Sections of the only known firsthand interview with P. N. Yakovlev, one of Michurin's assistants, is transcribed below.

From Michurin I. V. 1948. Sochineniya [Compositions]. 2nd Ed. Vol. II:

pg. 554 "The work on artificial crosses of mountain-ash was started by Michurin back in 1905. The first experimental material was our native *Sorbus aucuparia* and the black-fruited North American *Sorbus melanocarpa*. The cross became a new cultivar and was named by Michurin 'Likernaya'. It had quite edible black fruit suitable for preserves and beverages. After the [1917] October revolution, Michurin succeeded in producing extra-generic hybrids between *Sorbus*, *Crataegus*, *Pyrus*, and *Mespilus* and this started a number of new cultivars that far surpass the

pg. 555 species of mountain-ash so far known in western Europe and North America. Michurin's cultivars, such as 'Granatnaya', 'Dessertnaya', 'Lakovaya chernay', 'Burka' and others, are going to play major part as fruit shrubs and also as ornamental plants." During his late years, Michurin paid special attention to extra-generic hybridization of mountain-ashes with pears and apples, while trying to produce a larger-fruited mountain-ash."

"Producing hybrids between *Sorbus*, *Malus*, *Pyrus*, *Crataegus*, and *Mespilus* requires crossing en masse: not with hundreds, but rather with thousands or even scores of thousands of

pg. 556 flowers, which we attempted in 1934 for *Prunus besseyi* x *Amygdalus persica*."

pg. 557 "Sorbaronia is believed to be a hybrid of *Sorbus aucuparia* and *Sorbus aronia arbutifolia*. It is even less known than the previous ones." [Referring to intergeneric *Sorbus/Pyrus* and *Sorbus/Amelanchier* hybrids described but omitted in this translation]. "Upon receiving 'Likernaya' by crossing *S. aucuparia* x *S. melanocarpa*,

Michurin then produced a cross of 'Likernaya' with *Mespilus germanica* (1926). A seedling was obtained in 1927 and the first fruiting of the hybrid occurred in 1931. The hybrid looked more like *S. aucuparia* than anything else, only with wider leaflets and of dwarf general habit (no taller than 1.5 m at eight years old). One would not call it a tree. Indeed this is a sparse shrub, whose annual increment is less than 15-20 cm. The fruiting of the mother plant is weak: 3-4 inflorescences per year. In 1931 (the first fruiting year), a few scions were grafted onto a mature *S. aucuparia*. In 1934, the first good crop was produced. The fruits were dark red and tasted excellent. By July 15<sup>th</sup>, they already were so sweet that one could eat them right off the tree. By mid-August the fruits were completely ripe and good-tasted. The new cultivar was named 'Dessertnaya' by Michurin. The fruits were somewhat larger than in 'Likernaya' and of a beautiful dark red color, rather than black."

Michurin's notes, written mostly in shorthand, have lead to numerous interpretations of his works (Skvortsov et al., 1983). The fact is it was not entirely clear to Michurin what plant species he initially received from Germany, originally describing it only as a specimen of shrubby, black fruited mountain-ash. Only later did he classify this material as what modern authorities consider *A. melanocarpa*. Another problem in trying to follow Michurin's breeding work results from the discrepancy in nomenclature used during the period (Table 1). Michurin often refers to *Aronia* simply as "black-fruited mountain-ash" or "American *Sorbus*" leaving readers to infer the subject of which he is speaking is indeed *Aronia* based only on contextual descriptions of the plant material. What is clear is that prior to Michurin's experiments no records exist promoting it as a fruit crop, either in Germany from which he likely received plant material nor in Russia.

It was not until after Michurin's death in 1935 when Mikhail Lisavenko, a Michurin contemporary, obtained cuttings from Michurin's research facility in Michurinsk and began distributing and promoting them, that widespread cultivation began (Skvortsov et al., 1983). However, Lisavenko makes no mention of which varieties he collected from the Michurinsk facility. Attempts by Skvortsov (1983) to

obtain information from researchers at the station in Michurinsk proved unsuccessful. Eventually this germplasm would become widely planted throughout the Soviet Union.

Skvortsov et al. (1982 and 1983) could only speculate as to the hybrid ancestry of *A. mitschurinii* based on the contextual references noted in Michurin's works. With the dissolution of the Soviet Union, *Aronia* production dropped significantly, as did interest in developing new germplasm. Though limited production continued in former Eastern Bloc countries and Scandinavia (Jeppsson, 1999), *Aronia* remained relatively unknown as a crop in the west, and *A. mitschurinii* was never widely accepted nomenclature.

#### *American commercial Aronia production*

*Aronia mitschurinii* production in North America is chiefly centered in Wisconsin (Secher, 2005; Mulhern, 2008), Iowa (Sagario, 2008), the Pacific Northwest (King, 2001; Strik, 2003) and most recently in New England (Brand, production trials). *Aronia* is still a minor fruit crop with little acreage, so official production figures are not recorded by the U.S. Department of Agriculture. Figures reported by Sagario (2008) for Sawmill Hollow farm, a leading producer in Iowa, approach 40,000 lbs of fruit annually, with expectations for expanded production. Yields for *Aronia* average 22 lbs. per plant, with peaks up to 37 lbs. per plant (King, 2001) and returns between 8,000 and 10,000 U.S dollars per acre (Sagario, 2008). Plants are typically sold as rooted plugs and planted in rows 0.8 – 1 m apart (Mckay, 2001). Harvesting can be done mechanically using equipment and practices established for currants (*Ribes*)(Gatke and Wilke, 1991).

#### IV. Emerging Market

##### *Nutraceutical Value*

*Aronia mitschurinii* cultivation is increasing in the United States because of the discovery of exceedingly high levels of antioxidants present in fruits (Kahkonen et al., 1999; Kahkonen et al., 2001; Wu et al., 2004; Sagario, 2008; McWilliams, 2010; Cameron, 2010). Over the preceding decade the terms “nutraceutical” and “functional food” have become terms broadly classifying foods with significant health benefits beyond basic nutritional requirements. Antioxidants, in the form of phenolic compounds, are molecules that inhibit oxidation reactions and typically are included within this group. Antioxidants play important roles in reducing oxidative stress in cells. Diseases thought to have links to oxidative stress include alzheimer’s, parkinson’s, atherosclerosis and various cancers (Halliwell and Gutteridge, 1989).

As a defense against singlet oxygen species produced during cellular processes, plants have evolved organic antioxidants in the form of polyphenolic compounds. In *Aronia* these are typically flavonoids like anthocyanins and anthocyanidins that are commonly seen as the red and purple pigments in foliage and fruits. All higher plants contain various levels of flavonoids, but plants with dark-colored fruits are especially rich in these. Zheng and Wang (2003) compared the flavonoid and phenolic acid content of chokeberry to blueberry (*Vaccinium corymbosum*), cranberry (*Vaccinium macrocarpon*) and ligo berry (*Vaccinium vitis-idaea*). The study found that *Aronia melanocarpa* has the highest concentration of phenolic compounds, as well as the highest oxygen radical absorbance capacity (ORAC) of the four species studied. In a larger study, Agnieszka and Borowska (2008) compared phenolic levels in a number of



berry species and found *A. melanocarpa* to have 690 mg of polyphenols per 100 grams of fresh weight. Black chokeberry ranked above all species in the study and was higher than fruits touted for their antioxidant capacity, such as blueberry (*Vaccinium corymbosum*) (216-585 mg/100 g), blackberry (*Rubus fruticosus*) (415-555 mg/100 g) or cranberry (*Vaccinium macrocarpon*) (315 mg/100 g). Ovaskainen (2008) found similar results. Zheng and Wang (2003) found *Aronia* to have uniquely high concentrations of the anthocyanidins cyanidin 3-arabinoside, cyanidin 3-galactoside and plus high levels of the polyphenol, caffeic acid. Of the anthocyanidin aglycons found in *Aronia* (cyanidin, delphinidin, petunidin, malvidin and peronidin), the study found cyanidins had the highest ORAC. It is of the opinion of many authors that *Aronia*, with its high levels of phenolics and relative ease of production, has great potential to establish itself in the functional food market (Finn, 1999; King, 2001; McKay, 2001; Secher, 2005; Mulhern, 2008; Sagario, 2008; Brand, 2010; Cameron, 2010; McWilliams, 2010).

### *Medical research*

Modern interest in the health effects of *Aronia* from the medical community has been the focus of many peer reviewed studies (Gasiorowski et al., 1997; Faff and Frankiewicz-Jozko, 2003; Olas et al., 2008; Szajdek and Borowska, 2008; Kedzierska et al., 2009; Broncel et al., 2010; Chrubasik et al., 2010; Hellstrom et al., 2010; Kokotkiewicz et al., 2010; Olas et al., 2010). Historically, *Aronia* has been used by Native Americans for cold remedies and gastrointestinal problems (Smith, 1933; Kindscher and Hurlburt, 1998). More recently, the most promising studies have focused on the impacts chokeberry's antioxidants have on cardiovascular diseases (Hellstrom et

al., 2010) and cellular oxidative stress (Jurgonski et al., 2008). There is also some evidence *Aronia* anthocyanins have anti-mutagenic properties (Gasiorowski et al., 1997).

Hellstrom et al., (2010) studied anti-sclerotic properties of chokeberry juice. In Russia and Eastern Europe, folklore prescribed *Aronia* for the treatment of hypertension. In modern medicine angiotensin-converting enzyme, or ACE, inhibitors are commonly prescribed to regulate nitric oxide (NO) production, which is attributed to hypertension. Flavonoids, such as those present in *Aronia*, have been linked to the regulation of the same NO pathways (Bell et al., 2006). Hellstrom et al., (2010) found *Aronia* flavonoids to produce a significant short term reductions of blood pressure of up to 20/23 mm Hg (systolic/diastolic) for three hours after doses were given.

Broncel et al. (2010) conducted a clinical trial to determine chokeberry's effectiveness in combating oxidative stress resulting from obesity induced metabolic syndrome. In cases of chronic oxidative stress, naturally occurring antioxidative enzymes become degraded due to over use. After one month of a diet including *Aronia* significant decreases were recorded in thiobarbituric acid-reacting substrates or TBARS in patients with obesity induced metabolic syndrome, though levels did not reach those of the control group. TBARS are substances that directly contribute to degradation of cellular membranes through lipid peroxidation. Significant increases in our body's naturally occurring antioxidant enzymes, glutathione peroxidase and superoxide dismutase, were also observed in response to a diet containing *Aronia*.

Numerous studies similar to Broncel et al. (2010) and Hellstrom et al. (2010), linking chokeberry consumption to reduced blood pressure and oxidative stress, have

produced a compelling argument. However, research directly linking *Aronia* consumption to reduced instances of cancer are less substantiated. Gasiorowski et al. (1997) explored the ability of anthocyanins from *Aronia* to combat mutagenic activity of benzo( $\alpha$ )pyrene and 2-amino fluorene. The study found the flavonoids were able to scavenge sufficient reactive oxygen species to reduce rates of mutation. The research also found flavonoids to inhibit enzymes that activated promutagens. In contrast, Pool-Zobel et al. (1999) concluded that while flavonoids in *Aronia* are potent antioxidants and could reduce DNA strand breaks, no correlation could be made with respect to reduced base oxidation. Zhao et al. (2004) concluded that chokeberry extract significantly inhibited growth of a cancerous human colon cell line in an *in vitro* study. The study also demonstrated *Aronia* to reduce cell growth more than grape (*Vitis vinifera*) or bilberry (*Vaccinium myrtillus*). The body of research on the health benefits of *Aronia* consumption, though conflicting, is compelling. Larger clinical studies and further research would be helpful in determining if a more definitive link exists between *Aronia* consumption and cancer prevention (Chrubasik et al., 2010).

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**Table 1. Historical taxonomic treatments of *Aronia* species. A notation of (–) indicates that the species was not described by the author. For Heynhold (1841) *Sorbus floribunda* was recognized by Heynhold (1840) prior to formal inclusion of *Aronia* within *Sorbus*.**

Current nomenclature Campbell (2007)	Linnaeus, C (1753)	Linnaeus, F (1782)	Lamarck (1783)	Marshall (1785)	Medikus (1789)	Willdenow (1799)	Michaux (1803)	Persoon (1806)	Elliot (1821)
<i>Aronia</i>	in <i>Mespilus</i>	in <i>Pyrus</i>	in <i>Crataegus</i>	in <i>Mespilus</i>	<i>Aronia</i>	in <i>Pyrus</i>	in <i>Mespilus</i>	<i>Aronia</i>	<i>Aronia</i>
<i>arbutifolia</i>	<i>arbutifolia</i>	<i>arbutifolia</i>	<i>arbutifolia</i>	-	<i>arbutifolia</i>	<i>arbutifolia</i>	<i>arbutifolia</i>	<i>arbutifolia</i> & <i>pyrifolia</i>	-
<i>melanocarpa</i>	-	-	-	-	-	<i>arbutifolia</i> var. <i>nigra</i>	<i>arbutifolia</i> var. <i>melanocarpa</i>	-	<i>melanocarpa</i>
<i>prunifolia</i>	-	-	-	<i>prunifolia</i>	-	-	-	-	-

**Table 1. continued.**

Current nomenclature Campbell (2007)	Lindley (1826)	Heynhold (1841)	Wenzig (1883)	Focke (1888)	Koehne (1890)	Britton (1901)	Nieuwland (1915)	Rehder (1938)	Robertson & Phipps (1991)	Kalkman (2004)
<i>Aronia</i>	in <i>Pyrus</i>	in <i>Sorbus</i>	in <i>Sorbus</i> subd. <i>Aronia</i>	in <i>Pyrus</i> subg. <i>Aronia</i>	<i>Aronia</i>	<i>Aronia</i>	<i>Adenorachis</i>	<i>Aronia</i>	<i>Photinia</i>	<i>Aronia</i>
<i>arbutifolia</i>	-	<i>arbutifolia</i>	-	-	-	-	<i>arbutifolia</i>	-	<i>pyrifolia</i>	-
<i>melanocarpa</i>	-	<i>melanocarpa</i>	-	-	-	-	<i>melanocarpa</i>	-	<i>melanocarpa</i>	-
<i>prunifolia</i>	<i>floribunda</i>	<i>floribunda</i>	-	-	-	<i>atropurpurea</i>	<i>atropurpurea</i>	<i>prunifolia</i>	<i>floribunda</i>	-

Dash (-) indicates species not identified in publication.



Figure 1. Comparison of the habits of *Aronia melanocarpa* (left), and *Aronia mitschurinii* (right).



**Figure 2.** Comparison of leaf morphology of various *Aronia* species. Left to right: *Aronia arbutifolia*, *Aronia melanocarpa* (diploid), *Aronia melanocarpa* (tetraploid), *Aronia mitschurinii*.



**Figure 3.** Comparison of the fruits of *Aronia mitschurinii* (left), *Aronia melanocarpa* (right).

## **Chapter II**

### ***Aronia* Intergeneric Hybridization**

## Introduction

Wide hybridizations and allopolyploidy have been factors in speciation within the Pyrinae (Campbell et al., 1991; Campbell et al., 2007; Evans and Campbell, 2002; Robertson et al., 1991; Robertson et al., 2010). Intergeneric hybrids between *Crataegus* × *Mespilus*, *Cydonia* × *Pyrus*, and *Malus* × *Pyrus* have been documented, but the most frequently occurring intergeneric hybrids happen with the genus *Sorbus* (Robertson et al., 1991). Schneider (1906) described numerous intergeneric *Aronia* × *Sorbus* (×*Sorbaronia* C.K.Schneid) hybrids. Ivan Michurin (1948, 1949) also experimented with wide *Aronia* hybridization. Skvortsov et al. (1983) theorized that *Aronia mitschurinii* resulted from hybridization and polyploidization of *Aronia melanocarpa*. The focus of this chapter is to determine whether biological barriers prevent hybridization between *Aronia* and other genera within the Pyrinae. The first section describes ×*Sorbaronia* hybrids identified by Schneider (1906). The second section is the results from controlled crosses between *Aronia* and related species of Pyrinae.

## Aronia Intergeneric Hybrids

All known species of *Aronia* hybridize with one or more *Sorbus* species. These hybrids can be categorized roughly into two groups. The entire-leafed *Aronia* × *Sorbus aria* hybrids and the hybrids with deeply dissected leaf blades resulting from crosses with compound leaved *Sorbus* species. The ×*Sorbaronia* described in this section follow the treatments of Krussmann (1986), Schneider (1906), and Rehder (1920, 1940), though the authors disagree on or do not state crossing direction. To expand the



botanical descriptions in the literature, observations were made on herbarium and living specimens of  $\times$ *Sorbaronia* at the Arnold Arboretum of Harvard University (Boston, MA).

**$\times$ *Sorbaronia alpina*** (Willd.) Schneid. - *Aronia arbutifolia*  $\times$  *Sorbus aria*.

Specimens of  $\times$ *S. alpina* are present in living collections at the Arnold Arboretum and they are small to medium size trees of 5-7 m in height growing on a single or low branching trunk (Figure 1). These individuals do not match descriptions provided by Krussmann (1986), who described the hybrid as a 1-3 m shrub. The crown of  $\times$ *S. alpina* is symmetrical, oval in shape, becoming rounded and open with age. Young shoots and buds are tomentose. The inflorescence is a cyme, with flowers approximately the size of *S. aria*, pubescent, cream in color, styles 3-4 with a mildly pleasant fragrance inferred by *A. arbutifolia* (Figure 2). Leaf blades are elliptical to oblong, 5-7 cm long resembling that of *S. aria*, glabrous above, but densely pubescent below with glandular serration. Fruits are also very similar to *S. aria* and turn red to purple in the fall.

Growth rates for  $\times$ *S. alpina* reflect that of the *Sorbus*. A twenty-six year old accession (994-84) located in the Bradley Rosaceous Collection of the Arnold Arboretum had reached a height of 3-4 m. Sax (1932) determined that the  $\times$ *S. alpina* at the Arnold Arboretum to be triploid and of low fertility. Sax (1932) surmised that the height, which bears more similarity to *Sorbus* than to *Aronia*, was likely the result of the presence of two chromosome copies from *Sorbus* and a single chromosome copy from *Aronia*. Sax (1932) makes no mention that the height might have resulted from grafting and the accessions growing at the Arnold Arboretum did not possess an obvious graft union. Sax and Sax (1947) identified  $\times$ *S. alpina* as triploid, with 17 paired



chromosomes, and a number of unpaired, univalent chromosomes. This species also produced triploid flow cytometry profiles (Brand and Connolly, unpublished data). Pollen viability was reported from 0-24 percent depending on the anther selected. Open pollinated seeds collected by Sax and Sax (1947) failed to germinate. One significant detractor from this tree is its susceptibility to fireblight. Though not fatal to the tree, black shoots affected by fireblight were unattractive and induced early fruit drop. *Aronia* accessions growing in proximity to  $\times S. alpina$  did not exhibit any symptoms of the disease.

**$\times$ *Sorbaronia dippelii*** (Zab.) Schneid. - *Aronia melanocarpa*  $\times$  *Sorbus aria*. A living specimen (accession number 759-78) is present in the Bradley Rosaceous collection at the Arnold Arboretum. This hybrid, is a multi-stem shrub to small tree, that is shorter and more densely branched than  $\times S. alpina$  (Figure 3). Leaves are typically elliptic, thicker than those of *A. melanocarpa*, and possess white tomentum on the undersides resembling that of *S. aria* (Figure 4). Serration is similar to *Aronia* with dark glands on the teeth. The description by Krussmann (1986) is consistent with the specimen 759-78 at the Arnold Arboretum. Non-fragrant flowers are borne on lightly pubescent cymes that are slightly larger than those of *Aronia* (Figure 5). Fruits ripen in early to mid-September, are dark purple to black and morphologically similar to *S. aria*. Sax (1929) described  $\times S. dippelii$  as a diploid, and Sax and Sax (1947) indicated  $\times S. dippelii$  was pollen fertile, up to 58%, compared to *Aronia*, which was 76% pollen fertile. However, as with  $\times S. alpina$ , pollen germination was inconsistent between anthers. Sax and Sax (1947) found that  $\times S. dippelii$  could be used successfully as a

maternal parent in crosses with East Asian *Sorbus alnifolia*. I observed  $\times S. dippelii$  to exhibit a similar susceptibility to fireblight as  $\times S. alpina$ .

**$\times Sorbaronia fallax$**  Schneid. - *Aronia melanocarpa*  $\times$  *Sorbus aucuparia*. *Sorbus aucuparia* is a compound leaved *Sorbus* species making  $\times S. fallax$  the first of the  $\times Sorbaronia$  hybrids described in this section to possess deep foliar dissection (Figure 6).  $\times Sorbaronia fallax$  is described as a tree-like shrub by Rehder (1940) and Krussmann (1986) with branches outspread and nodding. Leaves are 3 – 8 cm long, partially ovate to oval-oblong and simple near the apex with dissection increasing in depth along the length, eventually becoming pinnately lobed towards the base. Blades are dark, glossy green above, and lightly tomentose beneath. Inflorescences are glabrous and hold flowers with 3-5 styles. Fruits are purple-black. Connolly (2009) documented the presence of glandular hairs along the upper side of leaf blade midribs, a characteristic typically considered distinctive of *Aronia*.

$\times Sorbaronia fallax$  has been documented to occur in many locations where the two species are sympatric (Connolly, 2009). I observed this hybrid growing feral at the St. Dennis Cemetery, 89 Kelton Road, Ashburnham, MA. At the site a landscape specimen of *S. aucuparia* had been planted and offspring had naturalized around the cemetery perimeter. Surrounding the cemetery were stands of *A. melanocarpa* growing together with lowbush blueberry (*Vaccinium angustifolium*). Along the wood line a number of  $\times S. fallax$  could be identified. A specimen from this site is currently being accessioned into the University of Connecticut herbarium.  $\times Sorbaronia fallax$  hybrids were determined based primarily by the irregular foliar dissection (Connolly, 2009). Plants were single stemmed, approximately 1 m in height, and noticeably taller than the

surrounding *A. melanocarpa*. Plants produced reddish-purple pomes, larger than those of *S. aucuparia* or *A. melanocarpa*.

Similar to  $\times S. fallax$  is  $\times Sorbaronia$  ‘Ivan’s Beauty’. This cultivar is a cross between *Sorbus aucuparia* and an unidentified species of black fruited chokeberry. Both  $\times S.$  ‘Ivan’s Beauty’ and  $\times S. fallax$  share a deeply dissected to compound leaf morphology. Fruits are typically larger and red to purple in color on  $\times S.$  ‘Ivan’s Beauty’. This cultivar is commercially available and occasionally cultivated as a novelty fruit crop.

**$\times Sorbaronia hybrida$**  (Moench) Schneid. - *Aronia arbutifolia*  $\times$  *Sorbus aucuparia*.  $\times Sorbaronia hybrida$  shares morphology with  $\times S. fallax$  with differences between the two correlating with defined differences seen in the two parental *Aronia* species. Krussmann (1986) describes identifying features including a greater degree of pubescent than  $\times S. fallax$ , and fruits that are purple, not ranging from purple to black as with  $\times S. fallax$ . The habit of  $\times S. hybrida$  is slightly larger than  $\times S. fallax$  and could be described as a shrub to small tree.

**$\times Sorbaronia sorbifolia$**  Poir. – *Aronia melanocarpa*  $\times$  *Sorbus americana*. This species is a naturally occurring hybrid in North America (Rehder, 1920). A mature specimen of  $\times S. sorbifolia$  can be found in the Bradley Rosaceous collection of the Arnold Arboretum (accession number 1239-85-A). This species also resembles  $\times S. fallax$  in morphology, but with more pointed leaf apices. The specimen observed at the Arnold Arboretum approached 3 m in height with an equal spread after 25 years, and had numerous basal stems. I observed fireblight was a problem on this species, causing stem die-back and leaf drop. In the absence of fireblight, Sax and Sax (1947) indicated

×*S. sorbifolia* to be a prolific fruiter, though with mostly aborted seeds. The species is diploid (Brand and Connolly, unpublished data) and pollen germination ranged from 0-50 percent depending on the anther examined (Sax and Sax, 1947). Sax and Sax (1947) reported of 50 open pollinated seedlings, 36 germinated and grew normally over a period of two years. The remainder either died or were significantly stunted. All seedlings were reported as possessing similar semi-compound leaf morphology (Sax and Sax, 1947).

×*Sorbaronia jackii* Rehd. - *Aronia prunifolia* × *Sorbus americana*. This is another naturally occurring hybrid that shares morphology with ×*S. fallax*, ×*S. hybrida*, and ×*S. sorbifolia*. The most notable difference identified by Krussmann (1986) are its lighter green leaves that are nearly glabrous on both surfaces. Leaflets are also described by Krussmann (1986) as more acuminate and ovate than ×*S. fallax*.

In their description of both ×*S. jackii* and ×*S. sorbifolia*, Sax and Sax (1947) do not provide any indication of the frequency at which hybrids occurs in the wild. *Sorbus americana* grows sympatrically with both *Aronia* species, but more commonly with *A. melanocarpa*. *Sorbus americana* and *A. melanocarpa* have likely developed biological barriers to hybridization that are not present in the more recently naturalized *S. aucuparia*. I have observed *S. americana* growing in proximity to *A. melanocarpa* in similar situations to that described at the Ashburnham, MA site where ×*S. fallax* was prolific, but could not find any ×*Sorbaronia*.

×*Sorbaronia arsenii* (Britt.) Jones – *Aronia melanocarpa* × *Sorbus decora*. This species was described by Jones (1939) as a small 1 – 2.5 m tall shrub with ascending branches. Leaf blades are deeply dissected to compound and similar to ×*S. fallax*.

Leaves range in length 2 – 7 cm, with an abruptly acute or shortly acuminate apex.

Pubescence on leaf undersides is slightly villous. Inflorescences are similar to that of *Aronia*; small and glabrous (Rehder, 1940). *Sorbus decora* is similar to *A. americana* in many respects, however *S. decora* is the more northern species making this hybrid more likely to occur at higher latitudes than  $\times S. sorbifolia$  or  $\times S. jackii$ . Reports of  $\times S. arsenii$  range from in upstate New York to Nova Scotia and Newfoundland (Jones, 1939; Rehder, 1940).

## Hybridization Experiments

The goal for this portion of my work was to explore what, if any genera within the Pyrinae can or will hybridize with *Aronia*, given its documented ability to hybridize with *Sorbus*. For those genera, such as *Sorbus*, that have been documented to hybridize with *Aronia*, my goal was to investigate the frequency of successful crosses and the optimal direction for crosses. It is hoped that this data can identify potential avenues for further germplasm improvements.

## Materials and Methods

### *Germplasm used in pollinations*

Detailed accession information for material used in this chapter is listed in table 1. *Aronia* accessions included in these experiments were pooled into pollination groups based upon species and ploidy. As established in chapter 1, *Aronia* exists in both diploid and tetraploid forms, with the latter exhibiting a high degree of apomixis. *Aronia* groups included *A. arbutifolia* tetraploid (4x), *A. melanocarpa* diploid (2x) and

*A. melanocarpa* tetraploid (4x). Pooling separate accessions into groups was useful due to limited numbers of individuals of any single accession and the greater likelihood of apomixis affecting gene flow as opposed to within species genetic variation. Results for all crosses are presented, however, the discussion focuses primarily on fruit set recorded for amphimictic maternal diploid *A. melanocarpa*.

***Sorbus*.** Within *Sorbus*, *S. aria* and *S. aucuparia* were selected for pollination studies based upon their known ability to hybridize with *Aronia* and other genera including *Cotoneaster* and *Pyrus* (Krussmann, 1986; Robertson et al., 1991). Ploidy levels of the specific *Sorbus* accessions utilized were unknown. Two East Asian *Sorbus*, *S. alnifolia* and *S. yuana* were included. *Sorbus alnifolia* is listed as a diploid (Dickson et al., 1992) and has been documented to hybridize with *Aronia* by Sax and Sax (1947). Sax and Sax (1947) only described the cross as successful, but do not describe the progeny. The North American species *S. americana* was also included since its ability to hybridize with *Aronia* has been well documented. This species exists as a diploid (Talent and Dickinson, 2005). A limited number of crosses were attempted with tetraploid *S. hybrid*, since a flowering specimen was available. All *Sorbus* accessions used in crosses were from the living collections of the Arnold Arboretum. Since both *Aronia* and *Sorbus* have been documented to hybridize, the goal here was to determine the optimal direction of crossing.

**×*Sorbaronia*.** Three ×*Sorbaronia* species, ×*S. alpina*, ×*S. dippelii*, and ×*S. sorbifolia*, were present in the collections of the Arnold Arboretum. An extensive number of backcrosses to *Aronia* were attempted with all of these individuals using multiple anthers to negate variability in pollen fertility described by Sax and Sax (1947).

The primary objectives of these crosses were to: 1) determine if  $F_1$   $\times$  *Sorbaronia* hybrids are fertile as Sax and Sax (1947) indicated; and 2) determine if any features unique to *A. mitschurinii* are present in  $F_2$  backcrosses to *Aronia*.

*Crataegus*, *Malus*, and *Pyrus* are species of great horticultural utility and are documented to hybridize amongst one another (Bell and Hough, 1986; Robertson et al., 1991). *Malus domestica* and *Pyrus communis* were included in hybridization studies because of their large, edible fruits and *Malus*  $\times$  *atrosanguinea* for its desirable ornamental features including fragrant pink flowers and red foliage. *Crataegus viridis* was included to determine if biological barriers exist to hybridization. In addition, some of *Aronia*'s desirable ornamental features (such as orange-red fall foliage color) could prove to be useful in producing a novel *Aronia*  $\times$  *Crataegus* genotype.

*Photinia* is a genus of shrubs and small trees native to the temperate regions of East Asia. *Photinia serrulata* and *Photinia*  $\times$  *fraseri* are broad leaved-evergreen shrubs reaching 4 m or more in height at maturity (Dirr, 2009). These species are cold hardy to zone 6 and grown widely in the southern United States as ornamentals. Both species possess distinctive red new shoot growth giving them their common name of red-tipped *Photinia*. Unfortunately, both species are highly susceptible to *Entomosporium*, a fungal pathogen causing leaf spotting and defoliation. *Photinia villosa* is a deciduous small tree species with stunning orange fall color. As with the evergreen species, *P. villosa* is highly susceptible to North American pathogens, specifically fireblight, and for that reason it is not widely grown as an ornamental. This genus also has modern taxonomic links to *Aronia* (Robertson et al., 1991).

The goal of crossing *Aronia* and *Photinia* is to determine if the two genera are sexually compatible. If crosses between *Aronia* and *Photinia* are successful, hybrids could be selected that would exhibit resistance to pathogens problematic for *Photinia*. In addition, certain ornamental features in a hybrid would be desirable including cold hardiness, fall foliage color, and shorter habit reflective of *Aronia*. *Aronia* plants could also be developed that would have longer fall leaf retention imparted by evergreen *Photinia* species.

*Amelanchier* often grows sympatric with *Aronia* and both are used as ornamentals. Early botanists often confused the two genera leading to numerous *Aronia* synonyms for *Amelanchier*. The two genera do share a superficial leaf morphology, flower structure, and apomixis. However, Campbell et al. (2007) resolved the two genera into distinct clades with high branch support, indicating any shared morphology is likely attributable to homoplasious evolution. Having co-evolved and developed into distinct clades within the Pyrinae, the goal of this cross is to test if the two genera have developed biological barriers to hybridization.

*Chaenomeles* and *Pseudocydonia* are East Asian genera of quince. *Chaenomeles*, and to a lesser extent *Pseudocydonia*, are commonly grown as woody ornamentals desired for their large, brightly colored early spring flowers or multi-colored bark. *Chaenomeles* is considered a diploid (Dirlewanger et al., 2009; Moffett, 1931) which would allow equal chromosome pairing in a cross with diploid *Aronia*. In addition to gametic compatibility, desirable ornamental features in an *Aronia* quince hybrid include large, showy flowers and habits similar to *Aronia*. Fireblight resistance would also be desirable as Dirr (2009) notes *Pseudocydonia* is highly susceptible.



### *Pollinations, plant care, and fruit harvesting*

Pollinations were performed April and May 2009 and 2010 at the University of Connecticut, Storrs, CT, the Arnold Arboretum of Harvard University, Boston, MA, and Scott Arboretum of Swarthmore College, Swarthmore, PA. Prior to bloom, containerized *Aronia* were held in dormancy over the winter in a minimally heated clear plastic, naturally lit, hoop greenhouse. Temperature in this greenhouse was set to 4°C to prevent freezing. Ventilation began at 13°C to prevent excessively high temperatures, potentially leading to bud break. When day time temperatures became unmanageable in the hoop greenhouse in early spring, plants were transferred to a dark cooler set at 4°C. To force growth and flowering, individual plants were removed from coolers and placed in a heated (18°C ± 9°C) glass greenhouse in a staggered manner to maintain a particular group in bloom continuously from April 1<sup>st</sup> until May 31<sup>st</sup>. Just prior to bloom plants were returned to the unheated (10°C ± 5°C) hoop greenhouse described above, which prolonged flowering. When available, accessions blooming at the University of Connecticut Plant Science Research Farm's *Aronia* field plantings were utilized as well.

Newly opened flowers for maternal individuals were emasculated by removing the anther from the filament. Pollen from selected paternal plants was transferred directly from a shedding anther to the receptive stigma. Inflorescences were then either bagged with brown paper bags or covered in aluminum foil for a period of 3-5 days to help facilitate fertilization and prevent open pollination. Pollinations conducted in greenhouses in the absence of pollinators were not covered. Container-grown accessions remained in greenhouses until fruit was set, were subsequently repotted, and

placed on trickle irrigation at the University of Connecticut Plant Science Research Farm for the growing season. Plants were fertilized with Osmocote® (formulation 17-6-10, 8-9 month) at the moderate label rate.

Fruit formation was observed to begin within one to two weeks following pollination. Fruits were monitored over the developmental period and harvested when ripe. Harvesting of *A. melanocarpa* fruits occurred from July to early August. *Aronia arbutifolia*, *Photinia* and *Sorbus* fruits were the last to be harvested in October. Fruits were allowed to soften for one week in shallow trays of water and then crushed to expel seeds. Seeds from 2009 and 2010 crosses were stratified in either 50ml Falcon® tubes or polyethylene Ziploc® bags at 5°C in moist sand for three months. After 90 days of stratification, seeds were germinated on Metro360® peat-based soilless potting medium in 32 oz ClearPac® salad trays with dome lids. The environment was 24°C ± 2°C with 16 hours of cool-white fluorescent light (40 µmol·m<sup>-2</sup>·s<sup>-1</sup>).

### *Tissue culture*

Attempts were made to circumvent dormancy requirements by excising embryos and germinating them *in vitro*. Preliminary attempts demonstrated that seedlings of *Aronia mitschurinii* ‘Viking’ could germinate if seed coats were removed and embryos placed on medium containing Murashige Skoog basal salts (Murashige and Skoog, 1962) supplemented with sucrose (30 g L<sup>-1</sup>), agar (7 g L<sup>-1</sup>) and pH adjusted to 5.7. This technique proved challenging for the smaller seeds of diploid *A. melanocarpa*, leading to a number of damaged embryos. The procedure was abandoned to avoid damaging valuable crosses. *Aronia* micropropagation medium (Brand and Cullina, 1992) was

utilized to rescue some confirmed hybrids post germination that exhibited extremely low vigor.

## **Results and Discussion**

### *Hybridizations*

Fruit and seed set data for both 2009 and 2010 are presented. Offspring from tetraploid maternal parents were found to be morphologically indistinguishable from the maternal parents in 2009, prompting the exclusion of polyploids as maternal parents in 2010. Only diploids determined by flow cytometry (Brand and Connolly, unpublished data) were used in this role in 2010. The fruit data presented in this section is based on the number of fruits present at harvest. Seeds that lacked noticeable endosperm or cotyledon development (unfilled) were determined to not be viable and were not included in tallies. Emasculation and bagging did not have a noticeable effect on fruit or seed set. Powdery mildew was present as a foliar pathogen on *Aronia*, but did not appear to be a factor affecting fruit set. However, for *Sorbus* and  $\times$ *Sorbaronia* growing at the Arnold Arboretum, winter moth and fireblight were present and likely contributed to fruit loss. *Aronia melanocarpa* accessions UC009, and UC010 demonstrated themselves to be the most useful maternal parents, producing seeds with large embryos and well developed endosperm. Both are diploid accessions collected in Damariscotta, ME. In total, 1839 flowers were pollinated leading to development of 404 fruits and 624 recovered seeds.

*Aronia* interspecific crosses set fruit at rates below those observed by Hardin (1973) (Table 2). Twenty-four diploid *A. melanocarpa* flowers pollinated with *A.*

*arbutifolia* produced a 50 % fruit set, yielding 32 viable seeds, or 2.6 per fruit. Sixty diploid *A. melanocarpa* flowers pollinated with *A. mitschurinii* produced only 33 % fruit set but averaged more seeds per fruit at 3.6. Twenty open pollinated diploid *A. melanocarpa* fruits yielded 55 seeds, an average of 2.75 per fruit. The flowers selected for controlled crosses were newly opened with few dehiscing anthers, which supports the protogyny described by Hardin (1973). However, the period was described by Hardin (1973) as not sufficiently long to effectively preclude fertilization and it is not believed to have had a significant effect on fruit set rates. Harden (1973) described *Aronia* to be autogamous, however, this data does not support this. Diploid *A. melanocarpa* flowers pollinated using anthers taken from the same plant abscised in a similar fashion as unpollinated flowers after two weeks. Controlled outcrosses on the same plant, under the same conditions, were observed to take within one week. Pistils on these flowers turned brown and petals fell within days of the cross.

***Sorbus*** demonstrated a significant ability to hybridize with *Aronia* (Table 3). One hundred twenty-six diploid *A. melanocarpa* flowers pollinated with *S. aria* pollen set fruit at a 33 % rate, producing 181 seeds. Twenty-four diploid *A. melanocarpa* flowers pollinated with *S. alnifolia* produced a fruit set rate of 70.8 %, yielding 45 seeds. Tetraploid *Aronia* pollinated with *Sorbus* pollen produced progeny identical to the maternal parent supporting the apogamous seed formation described by Persson-Hovmalm et al. (2004). Fruit and seed set rates for crosses involving *Sorbus* as a maternal parent varied considerably. *Sorbus aria*, pollinated using both diploid and tetraploid *A. melanocarpa* pollen, set only 2 fruits and no seeds out of a combined 84 attempts. The *S. aria* chosen for this cross developed fireblight during the growing

season and likely reduced the number of recoverable fruits. *Sorbus latifolia* pollinated with tetraploid *A. melanocarpa* produced progeny identical to the maternal *Sorbus*. *Sorbus alnifolia* set fruit at an 84.6 % rate when pollinated with diploid *A. melanocarpa*, producing 7 seeds on 11 fruits. When tetraploid pollen *A. melanocarpa* pollen was used in this role no viable seeds were recovered from the single fruit. *Sorbus yuana* set fruit at a 8.3 % rate when pollinated with diploid *A. melanocarpa*, however failed to produce any seeds. Tetraploid *A. melanocarpa* pollen crossed with maternal *S. yuana* yielded 7 seeds on 5 fruits. Relatively low fruit set rates for *S. yuana* are in contrast with the high rates for *S. alnifolia*, a similar species of East Asian origin. The ploidy status of *S. yuana* is unknown, but *S. alnifolia* is diploid (Dickson et al., 1992). Unequal chromosome pairing during fertilization is one potential explanation for the low crossing frequency if *S. yuana* is tetraploid. Fireblight was not observed on *S. alnifolia* and *S. yuana*. *Sorbus aucuparia* flowers pollinated with diploid *Aronia* produced 3 seeds on 4 fruits, however, fireblight was prevalent on the plant impacting fruit set. *Sorbus hybrida* set fruit at 16.7 % and 8.3 % using diploid and tetraploid *A. melanocarpa* respectively producing 4 and 1 fruits. However, fireblight and winter moth were also factors affecting crosses on this plant. Potential also exists for ploidy mismatches to affect fruit set rates. *Sorbus*, as with *Aronia*, exists in both diploid and tetraploid forms and was not addressed in documentation at the Arnold Arboretum. This data demonstrates diploid *Aronia* to be the more suitable maternal parent in crosses involving *Sorbus*.

×*Sorbaronia* exhibited a high degree of fertility as both a pollen and maternal parent (Table 4). One hundred forty maternal diploid *A. melanocarpa* flowers were pollinated and 67 fruits were recovered, producing a fruit set rate of 47.9%. Paternal

×*S. sorbifolia* had the highest fruit set on diploid *Aronia* at 66.6%, followed by ×*S. dippelii* at 60.8% and producing 50 and 132 seeds, respectively. ×*Sorbaronia alpina* also demonstrated a high rate of fruit set at 57.1 %, though significantly fewer crosses were attempted. ×*Sorbaronia* as a maternal parent produced much lower fruit sets. A significant factor contributing to this was prevalence of fireblight on these individuals. Maternal ×*S. 'Ivan's Beauty'* achieved a high rate of fruit formation after pollination, however few viable seeds were recovered from both the diploid and tetraploid *Aronia* crosses and all failed to germinate. Both ×*S. dippelii* and ×*S. sorbifolia* produced diploid flow cytometry profiles (Brand and Connolly, unpublished data) making these two the most logical crossing partners in future experiments.

***Crataegus, Malus, and Pyrus*** hybridizations produced mixed results (Tables 5-7). *Malus domestica* was the only one of the three genera to consistently induce fruit formation in diploid *A. melanocarpa* in both the 2009 and 2010 seasons. Attempts were made to pollinate *Malus* flowers by cutting the style halfway to the hypanthium and applying pollen to the cut surface. This technique did not result in any fruit formation on the apple and was not repeated on other species. Germination rates for putative *Aronia* × *Malus* hybrids was low, and morphology of these seedlings did not reveal obvious *Malus* morphology. *Pyrus* also did not induce fruit formation on diploid *A. melanocarpa*. In subsequent attempts at this cross, early stage fruit development has been observed.

***Photinia serrulata*** did hybridize with diploid *A. melanocarpa* to a limited extent (27.3%) and produced 4 seeds with well developed endosperm (Table 8). Ploidy levels for *P. serrulata* are undocumented, however polyploidy has been reported for *P. villosa*

(Moffett, 1931). A high degree of fruit set on *P. serrulata* in the absence of a pollinator is a characteristic of apomixis and tetraploidy. Additionally, all crosses involving *Photinia* as the maternal parent produced offspring indistinguishable from the maternal *Photinia* parent indicating these species reproduce apomictically. The interspecific hybrid *P. × fraseri* is a cross between *P. glabra* and *P. serrulata*, potentially making *P. glabra* diploid and *P. × fraseri* a triploid of unknown fertility. Open pollinated fruits from *P. × fraseri* persisted on the plant for a period of two months, but failed to reach maturity. Putative hybrids between *Aronia* and *P. serrulata* and *P. × fraseri* have thus far failed to germinate. Future crosses should involve *P. glabra* or other diploid *Photinia* to avoid ploidy mismatches.

***Amelanchier, Chaenomeles, and Pseudocydonia*** all failed to induce fruit formation on diploid *Aronia* (Tables 9-11). *Amelanchier × grandiflora*, a cross between diploid *A. arborea* and tetraploid *A. laevis*, was available as a pollen parent and, as expected, did not produce fruit set on diploid *A. melanocarpa* (Talent and Dickinson, 2005). The pollen fertility of *A. × grandiflora* is unknown, however mature fruits were prevalent on these plants. Diploid *Chaenomeles japonica* and *C. speciosa* (Dirlewanger et al. 2009; Moffett, 1931) were used in crosses. Diploid *Aronia* flowers pollinated by all three genera quickly turned yellow and fell off.

### *Morphology of Progeny*

Three controlled *×Sorbaronia dippelii* were successfully recovered from crosses made in the spring of 2009, two of which are shown in Figure 7. Confirmation of the hybrid nature of the seedlings was determined using the AFLP procedure described in

chapter 3 and by comparative morphology. The crosses were between maternal diploid *A. melanocarpa* UC007, an accession from Halls Pond, Chaplin, Connecticut, and *S. aria* var. *salicifolia* accession 222-27-A, a narrow leafed *S. aria* variety located at the Arnold Arboretum, Boston, MA. Vigor of the *A. melanocarpa* × *S. aria* var. *salicifolia* plants were significantly reduced when compared to an open pollinated seedling from the same maternal parent germinated on the same date. Under *in vitro* conditions, intergeneric seedlings demonstrated similar reductions in vigor in comparison to the open pollinated *Aronia* controls. Morphology was also distinct (Figures 8 and 9). Hybrid seedlings possessed deep foliar serration compared with open pollinated progeny of *A. melanocarpa* UC007.

Three additional intergeneric crosses between diploid *A. melanocarpa* UC007 and ×*Sorbaronia sorbifolia* were recovered using embryo rescue. Hybridity was confirmed by AFLP analysis (Chapter 3). The intergeneric diploid *A. melanocarpa* × ×*S. sorbifolia* hybrid seedlings were eventually established in containers in the greenhouse where they exhibited low vigor similar to the previously described ×*S. dippelii*. The leaves on the hybrid seedlings possessed deeper serrations than the leaves on diploid *A. melanocarpa*, but none of the foliar dissection characteristic of ×*S. sorbifolia* (Figure 10).



## Conclusions

This study identified intergeneric hybridizations as an approach for the development of novel *Aronia* germplasm. Four avenues for intergeneric hybridizations were identified: (1)  $\times$ *Sorbaronia* back crosses to diploid *Aronia*; (2) crosses between paternal *Sorbus* and diploid *A. melanocarpa*; (3) crosses between paternal *Malus domestica* and diploid *A. melanocarpa*; and (4) crosses between paternal *Photinia* and diploid *Aronia*.  $\times$ *Sorbaronia* is a well documented naturally occurring hybrid between *Aronia* and *Sorbus*, however the fertility of these intergeneric hybrids has been unknown. This study demonstrated the hybrids are of varying fertility and vigor, but can serve as a vector for transferring genetic material from *Sorbus*. Crosses between *Malus* and *Photinia* were successful in inducing fruit formation on diploid, amphimictic *Aronia* and have the potential to produce progeny that correct shortcomings in the various genera such as disease resistance and ornamental value. This study also supported findings of Persson-Hovmalm (2004) that apogamy is highly prevalent tetraploid *Aronia*, and in related *Pyrinae* genera.

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**Table 1. Accession information for germplasm used in controlled crosses. All *Aronia* are maintained in collections at the University of Connecticut Department of Plant Science research farm, other material is stored at the germplasm source listed. Ploidy status indicated by (?) is unknown.**

Accession ID	Germplasm Source	Accession Origin	Ploidy (2n = 2x = 17)
<i>Amelanchier canadensis</i>	Bassetts Bridge Rd, Mansfield Center, CT	Wild specimen	4x <sup>3</sup>
<i>Amelanchier</i> × <i>grandiflora</i>	University of Connecticut, Storrs, CT	Landscape specimen of cultivated origin	?
<i>Aronia arbutifolia</i> (4x)			
‘Brilliantissima’	Spring Meadow Nursery, Grand Haven, MI	Cultivated origin	4x <sup>1</sup>
‘Erecta’	ForestFarm, Williams, OR	Cultivated origin	4x <sup>1</sup>
PI578096	USDA, Ames, IA	Virginia	4x <sup>1</sup>
<i>Aronia melanocarpa</i> (2x)			
UC007	University of Connecticut, Storrs, CT	Halls pond, Chaplin, CT	2x <sup>1</sup>
UC009	University of Connecticut, Storrs, CT	Damariscotta lake, Nobleboro, ME	2x <sup>1</sup>
UC010	University of Connecticut, Storrs, CT	Damariscotta lake, Nobleboro, ME	2x <sup>1</sup>
UC015	University of Connecticut, Storrs, CT	Willington Bog, Rt. 320, Willington, CT	2x <sup>1</sup>
UC020	University of Connecticut, Storrs, CT	Mt. Battie, Camden, ME	2x <sup>1</sup>
UC022	University of Connecticut, Storrs, CT	Pachaug State Forest, Voluntown, CT	2x <sup>1</sup>
UC030	University of Connecticut, Storrs, CT	TNC property, Salem, CT	2x <sup>1</sup>
UC034	University of Connecticut, Storrs, CT	Steuben, ME	2x <sup>1</sup>
UC037	University of Connecticut, Storrs, CT	Pachaug State Forest, Voluntown, CT	2x <sup>1</sup>
PI613016	USDA, Ames, IA	Massachusetts	2x <sup>1</sup>
<i>Aronia melanocarpa</i> (4x)			
‘Elata’	ForestFarm, Williams, OR	Cultivated origin	4x <sup>1</sup>
AMES27615	USDA, Ames, IA	Minnesota	4x <sup>1</sup>
PI545687	USDA, Ames, IA	Michigan	4x <sup>1</sup>
PI603106	USDA, Ames, IA	Tennessee	4x <sup>1</sup>
PI618684	USDA, Ames, IA	Wisconsin	4x <sup>1</sup>
<i>Aronia mitschurinii</i>			
‘Nero’	Spring Meadow Nursery, Grand Haven, MI	Cultivated origin	4x <sup>1</sup>
‘Viking’	Spring Meadow Nursery, Grand Haven, MI	Cultivated origin	4x <sup>1</sup>
<i>Aronia prunifolia</i>			
AMES27010	USDA, Ames, IA	Michigan	4x <sup>1</sup>
PI603107	USDA, Ames, IA	Virginia	4x <sup>1</sup>
<i>Chaenomeles japonica</i>	Leonard residence, Chelmsford, MA	Landscape specimen of cultivated origin	2x <sup>3</sup>
<i>Chaenomeles speciosa</i>	University of Connecticut, Storrs, CT	Landscape specimen of cultivated origin	2x <sup>2</sup>
<i>Crataegus viridis</i> ‘Winter King’	University of Connecticut, Storrs, CT	Landscape specimen of cultivated origin	2x <sup>7</sup>
<i>Malus</i> × <i>atrosanguinea</i>	University of Connecticut, Storrs, CT	Landscape specimen of cultivated origin	?

<i>Malus domestica</i>			
‘Cameo’	Wright Orchard, Willington, CT	Orchard specimen of cultivated origin	2x <sup>2</sup>
‘Hidden Rose’	University of Connecticut, Storrs, CT	Ornamental specimen of cultivated origin	2x <sup>2</sup>
‘Macoun’	Wright Orchard, Willington, CT	Orchard specimen of cultivated origin	2x <sup>2</sup>
‘Red Delicious’	Wright Orchard, Willington, CT	Orchard specimen of cultivated origin	2x <sup>2</sup>
<i>Photinia</i> × <i>fraserii</i>		Cultivated origin	?
<i>Photinia serrulata</i>	Scott arboretum, Swarthmore, PA	Unknown origin	?
<i>Photinia villosa</i>	University of Connecticut, Storrs, CT	Landscape specimen	4x <sup>3</sup>
<i>Pseudocydonia sinensis</i>	University of Connecticut, Storrs, CT	Landscape specimen	?
<i>Pyrus communis</i> ‘Bartlett’	Leonard residence, Chelmsford, MA	Orchard specimen of cultivated origin	2x <sup>3</sup>
<i>Sorbus alnifolia</i>	Arnold Arboretum, Boston, MA	Royal Botanical Garden, Kew, England	2x <sup>8</sup>
<i>Sorbus aria</i> var. <i>salicifolia</i>			
222-27-A	Arnold Arboretum, Boston, MA	Royal Botanical Garden, Edinburgh, Scotland	2x <sup>6</sup>
260-70-A	Arnold Arboretum, Boston, MA	Royal Botanical Garden, Edinburgh, Scotland	2x <sup>6</sup>
<i>Sorbus aucuparia</i>	Arnold Arboretum, Boston, MA	Hiller Nurseries, England	2x <sup>6</sup>
<i>Sorbus hybrida</i>	Arnold Arboretum, Boston, MA	Belmonte Arboretum, Netherlands	4x <sup>6</sup>
<i>Sorbus latifolia</i>	Arnold Arboretum, Boston, MA	Vilmorin-Andrieux, France	4x <sup>6</sup>
<i>Sorbus yuana</i>			
1539-80-C	Arnold Arboretum, Boston, MA	W. Hubei Shennongjia Forest District, China	?
1894-80-C	Arnold Arboretum, Boston, MA	W. Hubei Shennongjia Forest District, China	?
× <i>Sorbaronia</i> ‘Ivan’s Beauty’	University of Connecticut, Storrs, CT	Cultivated origin	?
× <i>Sorbaronia alpina</i>			
98-91-B	Arnold Arboretum, Boston, MA		3x <sup>5</sup>
994-84-A	Arnold Arboretum, Boston, MA	Royal Botanical Garden, Kew, England	3x <sup>5</sup>
× <i>Sorbaronia dippelii</i>	Arnold Arboretum, Boston, MA	Simon-Louis Freres, Germany	2x <sup>4</sup>
× <i>Sorbaronia sorbifolia</i>	Arnold Arboretum, Boston, MA	Nova Scotia, Canada	2x <sup>1</sup>

<sup>1</sup>Brand and Connolly, unpublished flow cytometry data on University of Connecticut collections. <sup>2</sup>Dirlewanger et al. (2009). <sup>3</sup>Moffett (1931). <sup>4</sup>Sax (1929).

<sup>5</sup>Sax (1932). <sup>6</sup>Nelson-Jones et al. (2002). <sup>7</sup>Talent and Dickinson (2005). <sup>8</sup>Dickson et al. (1992).

**Table 2. *Aronia* crosses with *Aronia*. Missing values are indicated by a dash (-). Frequency is calculated as the difference between the number of fruits collected from the number of flowers pollinated.**

Maternal	Paternal	Flowers pollinated	Fruits	Frequency (%)	Seeds	Seeds per fruit
<i>Aronia melanocarpa</i> 2x <sup>1</sup>	Open	-	20	-	55	2.75
<i>Aronia melanocarpa</i> 2x <sup>2</sup>	Self	9	0	0	0	0
<i>Aronia melanocarpa</i> 2x <sup>2</sup>	<i>Aronia arbutifolia</i> 4x <sup>3</sup>	24	12	50	32	2.6
<i>Aronia melanocarpa</i> 2x <sup>2</sup>	<i>Aronia mitschurinii</i> <sup>4</sup>	60	20	33	72	3.6
<i>Aronia mitschurinii</i> <sup>4</sup>	<i>Aronia melanocarpa</i> 2x <sup>2</sup>	16	8	50	15	1.88

<sup>1</sup>UC009. <sup>2</sup>UC010. <sup>3</sup>'Brilliantissima'. <sup>4</sup>'Viking'.

**Table 3. *Aronia* crosses with *Sorbus*. Frequency is calculated as the difference between the number of fruits collected and the number of flowers pollinated.**

Maternal	Paternal	Flowers pollinated	Fruits	Frequency (%)	Seeds
<i>Aronia melanocarpa</i> 2x <sup>1</sup>	<i>Sorbus aria</i> <sup>2</sup>	126	42	33.3	181
<i>Aronia melanocarpa</i> 4x <sup>3</sup>	<i>Sorbus aria</i> <sup>2</sup>	76	33	43.4	8
<i>Sorbus aria</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 2x <sup>4</sup>	24	0	0	0
<i>Sorbus aria</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 4x <sup>5</sup>	60	2	3.3	0
<i>Sorbus latifolia</i> <sup>6</sup>	<i>Aronia melanocarpa</i> 4x <sup>5</sup>	28	12	42.9	0
<i>Aronia melanocarpa</i> 2x <sup>7</sup>	<i>Sorbus alnifolia</i> <sup>8</sup>	24	17	70.8	45
<i>Aronia melanocarpa</i> 4x <sup>9</sup>	<i>Sorbus alnifolia</i> <sup>8</sup>	35	24	68.6	23
<i>Sorbus alnifolia</i> <sup>8</sup>	<i>Aronia melanocarpa</i> 2x <sup>10</sup>	13	11	84.6	7
<i>Sorbus alnifolia</i> <sup>8</sup>	<i>Aronia melanocarpa</i> 4x <sup>5</sup>	25	1	4.0	0
<i>Aronia arbutifolia</i> 4x <sup>11</sup>	<i>Sorbus yuana</i> <sup>12</sup>	14	13	92.9	0
<i>Aronia melanocarpa</i> 4x <sup>9</sup>	<i>Sorbus yuana</i> <sup>12</sup>	16	13	81.3	1
<i>Sorbus yuana</i> <sup>13</sup>	<i>Aronia arbutifolia</i> 4x <sup>12</sup>	14	3	21.4	10
<i>Sorbus yuana</i> <sup>12</sup>	<i>Aronia melanocarpa</i> 2x <sup>10</sup>	12	1	8.3	0
<i>Sorbus yuana</i> <sup>14</sup>	<i>Aronia melanocarpa</i> 4x <sup>5</sup>	26	5	19.2	7
<i>Sorbus aucuparia</i> <sup>15</sup>	<i>Aronia melanocarpa</i> 2x <sup>16</sup>	19	4	21.1	3
<i>Sorbus hybrida</i> <sup>17</sup>	<i>Aronia melanocarpa</i> 2x <sup>16</sup>	18	3	16.7	4
<i>Sorbus hybrida</i> <sup>17</sup>	<i>Aronia melanocarpa</i> 4x <sup>5</sup>	12	1	8.3	1
<b>Total for all crosses</b>		<b>542</b>	<b>185</b>	<b>34.1</b>	<b>290</b>
<b>Total for maternal <i>Aronia melanocarpa</i> 2x only</b>		<b>150</b>	<b>59</b>	<b>39.3</b>	<b>226</b>

<sup>1</sup>UC009, UC010, and PI613016. <sup>2</sup>AA260-70-A, and AA222-27-A. <sup>3</sup>AMES27615, and 'Morton'. <sup>4</sup>PI613016, and UC010. <sup>5</sup>PI618684. <sup>6</sup>AA18462-B.

<sup>7</sup>UC007, and PI613016. <sup>8</sup>AA1497-52-B and AA1300-61-B. <sup>9</sup>AMES27615. <sup>10</sup>PI613016. <sup>11</sup>'Brilliantissima'. <sup>12</sup>AA1539-80-D. <sup>13</sup>AA1894-80-6.

<sup>14</sup>AA1894-80-6 13, and AA1539-80-D. <sup>15</sup>AA180-57-A. <sup>16</sup>UC010. <sup>17</sup>AA1119-65-A.



**Table 4. *Aronia* crosses with  $\times$ Sorbaronia.**

Maternal	Paternal	Flowers pollinated	Fruits	Frequency (%)	Seeds
<i>Aronia arbutifolia</i> 4x <sup>1</sup>	$\times$ Sorbaronia alpina <sup>2</sup>	22	1	4.5	0
<i>Aronia melanocarpa</i> 2x <sup>3</sup>	$\times$ Sorbaronia alpina <sup>4</sup>	7	4	57.1	6
<i>Aronia melanocarpa</i> 4x <sup>3</sup>	$\times$ Sorbaronia alpina <sup>2</sup>	29	0	-	-
$\times$ Sorbaronia alpina <sup>5</sup>	<i>Aronia arbutifolia</i> 4x <sup>1</sup>	33	9	27.3	1
$\times$ Sorbaronia alpina <sup>4</sup>	<i>Aronia melanocarpa</i> 2x <sup>3</sup>	46	2	4.3	3
$\times$ Sorbaronia alpina <sup>2</sup>	<i>Aronia melanocarpa</i> 4x <sup>6</sup>	27	4	14.8	0
<i>Aronia melanocarpa</i> 2x <sup>7</sup>	$\times$ Sorbaronia dippelii <sup>8</sup>	69	42	60.8	132
$\times$ Sorbaronia dippelii <sup>8</sup>	<i>Aronia melanocarpa</i> 2x <sup>9</sup>	50	13	26.0	27
$\times$ Sorbaronia dippelii <sup>8</sup>	<i>Aronia melanocarpa</i> 4x <sup>6</sup>	21	4	19.0	5
<i>Aronia melanocarpa</i> 2x <sup>10</sup>	$\times$ Sorbaronia sorbifolia <sup>11</sup>	30	20	66.6	50
$\times$ Sorbaronia sorbifolia <sup>11</sup>	<i>Aronia melanocarpa</i> 2x <sup>3</sup>	27	1	3.7	1
$\times$ Sorbaronia sorbifolia <sup>11</sup>	<i>Aronia melanocarpa</i> 4x <sup>6</sup>	16	0	-	-
<i>Aronia melanocarpa</i> 2x <sup>3</sup>	$\times$ S. 'Ivan's Beauty'	34	1	2.9	1
<i>Aronia melanocarpa</i> 4x <sup>6</sup>	$\times$ S. 'Ivan's Beauty'	36	9	25.0	2
$\times$ S. 'Ivan's Beauty'	<i>Aronia melanocarpa</i> 2x <sup>13</sup>	26	6	23.0	1
$\times$ S. 'Ivan's Beauty'	<i>Aronia melanocarpa</i> 4x <sup>6</sup>	57	52	91.2	2
<b>Total for all crosses</b>		<b>530</b>	<b>168</b>	<b>31.7</b>	<b>231</b>
<b>Total for maternal <i>Aronia melanocarpa</i> 2x only</b>		<b>140</b>	<b>67</b>	<b>47.9</b>	<b>189</b>

<sup>1</sup>'Brilliantissima'. <sup>2</sup>AA98-91-B. <sup>3</sup>UC007. <sup>4</sup>AA994-84-A. <sup>5</sup>AA98-91-1, AA994-84-A 20. <sup>6</sup>PI618684. <sup>7</sup>UC009. <sup>8</sup>AA759-78. <sup>9</sup>UC010, and PI613016.

<sup>10</sup>UC009. <sup>11</sup>AA1239-85-A. <sup>13</sup>613016.

**Table 5. *Aronia* crosses with *Crataegus*.**

Maternal	Paternal	Flowers pollinated	Fruits	Frequency (%)	Seeds
<i>Aronia arbutifolia</i> 4x <sup>1</sup>	<i>Crataegus viridis</i> <sup>2</sup>	18	3	16.7	0
<i>Aronia melanocarpa</i> 4x <sup>3</sup>	<i>Crataegus viridis</i> <sup>2</sup>	20	17	85.0	0
<i>Crataegus viridis</i> <sup>2</sup>	<i>Aronia arbutifolia</i> 4x <sup>1</sup>	19	3	15.8	0
<i>Crataegus viridis</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 2x <sup>4</sup>	11	0	-	-
<i>Crataegus viridis</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 4x <sup>5</sup>	18	0	-	-
<b>Total for all crosses</b>		<b>86</b>	<b>23</b>	<b>39.2</b>	<b>0</b>

<sup>1</sup>PI578096. <sup>2</sup>'Winter King'. <sup>3</sup>PI618684. <sup>4</sup>PI613016. <sup>5</sup>PI603106.

**Table 6. *Aronia* crosses with *Malus*.**

Maternal	Paternal	Flowers pollinated	Fruits	Frequency (%)	Seeds
<i>Aronia melanocarpa</i> 2x <sup>1</sup>	<i>Malus</i> × <i>atrosanguinea</i> <sup>2</sup>	7	0	-	-
<i>A. melanocarpa</i> 4x <sup>3</sup>	<i>Malus</i> × <i>atrosanguinea</i> <sup>2</sup>	5	0	-	-
<i>Malus</i> × <i>atrosanguinea</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 2x <sup>4</sup>	30	0	-	-
<i>Malus</i> × <i>atrosanguinea</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 4x <sup>3</sup>	26	0	-	-
<i>Aronia arbutifolia</i> 4x <sup>5</sup>	<i>Malus domestica</i> <sup>6</sup>	8	0	-	-
<i>Aronia melanocarpa</i> 2x <sup>7</sup>	<i>Malus domestica</i> <sup>6</sup>	50	15	30.0	52
<i>Aronia mitschurinii</i> 4x <sup>8</sup>	<i>Malus domestica</i> <sup>9</sup>	32	19	59.4	34
<i>Malus domestica</i> <sup>10</sup>	<i>Aronia melanocarpa</i> 2x <sup>11</sup>	52	0	-	-
<b>Total for all crosses</b>		<b>210</b>	<b>34</b>	<b>16.2</b>	<b>86</b>
<b>Total for maternal <i>Aronia melanocarpa</i> 2n only</b>		<b>57</b>	<b>15</b>	<b>26.3</b>	<b>52</b>

<sup>1</sup>UC037. <sup>2</sup>Landscape specimen, University of Connecticut, Storrs, CT. <sup>3</sup>PI545687. <sup>4</sup>UC010. <sup>5</sup>'Erecta'. <sup>6</sup>'Hidden rose', 'Macoun', 'Cameo' and 'Red delicious'. <sup>7</sup>UC009, and PI613016. <sup>8</sup>'Viking'. <sup>9</sup>'Macoun' and 'Cameo'. <sup>10</sup>'Hidden rose', 'Macoun' and 'Cameo'. <sup>11</sup>UC022, UC034, and PI613016.

**Table 7. *Aronia* crosses with *Pyrus*.**

Maternal	Paternal	Flowers pollinated	Fruits	Seeds
<i>Aronia melanocarpa</i> 2x <sup>1</sup>	<i>Pyrus communis</i> <sup>2</sup>	11	0	-
<i>Pyrus communis</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 2x <sup>3</sup>	3	0	-
<i>Pyrus communis</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 4x <sup>4</sup>	5	0	-
<b>Total for all crosses</b>		<b>19</b>	<b>0</b>	<b>0</b>

<sup>1</sup>UC015, and UC030. <sup>2</sup>‘Bartlett’. <sup>3</sup>UC015. <sup>4</sup>PI545687.

**Table 8. *Aronia* crosses with *Photinia*.**

Maternal	Paternal	Flowers pollinated	Fruits	Frequency (%)	Seeds
<i>Aronia arbutifolia</i> 4x <sup>1</sup>	<i>Photinia serrulata</i> <sup>2</sup>	29	0	-	-
<i>Aronia melanocarpa</i> 2x <sup>3</sup>	<i>Photinia serrulata</i> <sup>2</sup>	11	3	27.3	4
<i>Aronia melanocarpa</i> 4x <sup>4</sup>	<i>Photinia serrulata</i> <sup>2</sup>	15	1	6.7	0
<i>Photinia serrulata</i> <sup>2</sup>	<i>Aronia arbutifolia</i> 4x <sup>1</sup>	15	1	6.7	0
<i>Photinia serrulata</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 2x <sup>5</sup>	39	11	28.2	-
<i>Photinia serrulata</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 4x <sup>4</sup>	16	1	6.3	-
<i>Photinia</i> × <i>fraseri</i>	<i>Aronia arbutifolia</i> 4x <sup>1</sup>	16	0	-	-
<i>Photinia</i> × <i>fraseri</i>	<i>Aronia melanocarpa</i> 2x <sup>3</sup>	13	0	-	-
<i>Aronia arbutifolia</i> 4x <sup>6</sup>	<i>Photinia villosa</i> <sup>7</sup>	11	1	9.1	0
<i>Aronia melanocarpa</i> 2x <sup>3</sup>	<i>Photinia villosa</i> <sup>7</sup>	24	0	-	0
<i>Aronia melanocarpa</i> 4x <sup>7</sup>	<i>Photinia villosa</i> <sup>7</sup>	16	11	68.8	9
<i>Photinia villosa</i> <sup>7</sup>	<i>Aronia arbutifolia</i> 4x <sup>6</sup>	39	9	23.0	3
<i>Photinia villosa</i> <sup>7</sup>	<i>Aronia melanocarpa</i> 2x <sup>3</sup>	15	1	6.7	1
<i>Photinia villosa</i> <sup>7</sup>	<i>Aronia melanocarpa</i> 4x <sup>8</sup>	14	2	14.3	0
<b>Total for all crosses</b>		<b>273</b>	<b>41</b>	<b>15.0</b>	<b>17</b>
<b>Total for maternal <i>Aronia melanocarpa</i> 2n only</b>		<b>11</b>	<b>3</b>	<b>6.7</b>	<b>4</b>

<sup>1</sup>‘Brilliantissima’. <sup>2</sup>SA91-589. <sup>3</sup>UC010. <sup>4</sup>PI545687. <sup>5</sup>UC010, and UC015. <sup>6</sup>PI578096, and ‘Brilliantissima’. <sup>7</sup>Landscape specimen, University of Connecticut, Storrs, CT. <sup>8</sup>PI618684.

**Table 9. *Aronia* crosses with *Amelanchier*.**

Maternal	Paternal	Flowers pollinated	Fruits set
<i>Aronia arbutifolia</i> 4x <sup>1</sup>	<i>Amelanchier</i> × <i>grandiflora</i> <sup>2</sup>	4	0
<i>Aronia melanocarpa</i> 2x <sup>3</sup>	<i>Amelanchier</i> × <i>grandiflora</i> <sup>2</sup>	6	0
<i>Aronia melanocarpa</i> 4x <sup>4</sup>	<i>Amelanchier</i> × <i>grandiflora</i> <sup>2</sup>	9	0
<i>Amelanchier canadensis</i> <sup>5</sup>	<i>Aronia melanocarpa</i> 4x <sup>4</sup>	4	0
<b>Total for all crosses</b>		23	0

<sup>1</sup>'Brilliantissima'. <sup>2</sup>Landscape specimen, University of Connecticut, Storrs, CT. <sup>3</sup>UC010. <sup>4</sup>PI545687. <sup>5</sup>Wild specimen, Bassetts Bridge Rd, Mansfield Center, CT.

**Table 10. *Aronia* crosses with *Chaenomeles*.**

Maternal	Paternal	Flowers pollinated	Fruits	Frequency (%)	Seeds
<i>Aronia arbutifolia</i> 4x <sup>1</sup>	<i>Chaenomeles speciosa</i> <sup>2</sup>	24	1	4.2	0
<i>Aronia melanocarpa</i> unknown x <sup>3</sup>	<i>Chaenomeles speciosa</i> <sup>2</sup>	5	0	-	-
<i>Aronia melanocarpa</i> 4x <sup>4</sup>	<i>Chaenomeles speciosa</i> <sup>2</sup>	44	4	9.1	0
<i>Chaenomeles speciosa</i> <sup>2</sup>	<i>Aronia arbutifolia</i> 4x <sup>5</sup>	4	0	-	-
<i>Chaenomeles speciosa</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 2x <sup>6</sup>	2	0	-	-
<i>Chaenomeles speciosa</i> <sup>2</sup>	<i>Aronia melanocarpa</i> 4x <sup>7</sup>	14	0	-	-
<i>Aronia melanocarpa</i> 2x <sup>8</sup>	<i>Chaenomeles japonica</i> <sup>9</sup>	10	0	-	-
<i>Aronia melanocarpa</i> 4x <sup>10</sup>	<i>Chaenomeles japonica</i> <sup>9</sup>	9	0	-	-
<i>Chaenomeles japonica</i> <sup>9</sup>	<i>Aronia arbutifolia</i> 4x <sup>5</sup>	2	0	-	-
<i>Chaenomeles japonica</i> <sup>9</sup>	<i>Aronia melanocarpa</i> 2x <sup>8</sup>	22	0	-	-
<i>Chaenomeles japonica</i> <sup>9</sup>	<i>Aronia melanocarpa</i> 4x <sup>7</sup>	7	0	-	-
<b>Total for all crosses</b>		<b>143</b>	<b>5</b>	<b>3.5</b>	<b>0</b>

<sup>1</sup>'Erecta', and PI578096. <sup>2</sup>Landscape specimen, University of Connecticut, Storrs, CT. <sup>3</sup>UC037. <sup>4</sup>'Elata', and PI545687. <sup>5</sup>'Brilliantissima'. <sup>6</sup>UC009. <sup>7</sup>PI545687, and 'Elata'. <sup>8</sup>UC015. <sup>9</sup>Landscape specimen, Leonard residence, Chelmsford, MA. <sup>10</sup>PI545687.

**Table 11. *Aronia* crosses with *Pseudocydonia*.**

<b>Maternal</b>	<b>Paternal</b>	<b>Flowers pollinated</b>	<b>Fruits set</b>	<b>Seeds</b>
<i>Aronia melanocarpa</i> 2x <sup>1</sup>	<i>Pseudocydonia sinensis</i> <sup>2</sup>	13	0	-
		13	0	-

<sup>1</sup>UC010. <sup>2</sup> Landscape specimen, University of Connecticut, Storrs, CT.



**Figure 1.** Mature habit of *×Sorbaronia alpina* (*Aronia arbutifolia*  $\times$  *Sorbus aria*) growing in the living collections of the Arnold Arboretum of Harvard University, Boston, MA. Accession number 994-84-A.



**Figure 2. Inflorescence of *×Sorbaronia alpina* accession number 994-84-A, living collections of the Arnold Arboretum of Harvard University, Boston, MA.**





**Figure 3. Mature habit of *xSorbaronia dippelii* (*Aronia melanocarpa* × *Sorbus aria*) growing in the living collections of the Arnold Arboretum of Harvard University, Boston, MA. Accession number 759-78.**



**Figure 4. Leaf morphology of *xSorbaronia dippelii* accession number 759-78, living collections of the Arnold Arboretum of Harvard University, Boston, MA.**





**Figure 5. Inflorescence of *×Sorbaronia dippelii* accession number 759-78, living collections of the Arnold Arboretum of Harvard University, Boston, MA.**



Figure 6. Herbarium specimen of  $\times$ Sorbaronia fallax (*Aronia melanocarpa*  $\times$  *Sorbus aucuparia*) accession number 19694, Arnold Arboretum Herbarium, Boston, MA. Notice irregular foliar dissection reflective of a hybrid between simple and compound leaved species.



**Figure 7.** Comparison in vigor between  $\times$ *Sorbaronia dippelii* UC125 and UC126 (left and center) and open pollinated *Aronia melanocarpa* UC007 (right). Accessions UC125 and UC126 are  $F_1$  hybrids between *Aronia melanocarpa* UC007 and *Sorbus aria* var. *salicifolia* accession 222-27-A, Arnold Arboretum, Boston, MA.





Figure 8. Rooted cuttings of open pollinated *Aronia melanocarpa* UC007, four weeks ex vitro. Foliar serration typical of *Aronia melanocarpa*.



Figure 9. Rooted cuttings of *xSorbaronia dippelii* UC125, four weeks ex vitro. Foliar serration are significantly more pronounced than on *Aronia melanocarpa*.



**Figure 10.** *Aronia melanocarpa* UC007  $\times$  *Sorbaronia sorbifolia* 1239-85-C, Arnold Arboretum, Boston, MA. Plants are mid way through the second growing season. Note lack of foliar dissection characteristic of *Sorbaronia sorbifolia*.

### **Chapter III**

#### **Assessment of the Genetic Relationship of *Aronia mitschurinii* to Wild North American *Aronia* Species Using AFLP Analysis.**

## Introduction

*Aronia* is a taxonomically complex genus that holds substantial promise for expanded use as both an ornamental and fruit crop. Native North American *Aronia* species include *A. arbutifolia* (L.) Pers., red chokeberry, *A. melanocarpa* (Michx.) Elliot, black chokeberry and, *A. prunifolia* (Marsh.) Rehder, purple chokeberry. The third species, *A. prunifolia*, is generally accepted as a naturally occurring, interspecific hybrid, although this assumption is not well-documented with research evidence (Rehder, 1920; Dirr, 2009).

A fourth species, *Aronia mitschurinii* (A.K.Skvortsov & Maitul.), has also been proposed and is the focus of this work. Most North American sources treat *A. mitschurinii* as a cultivar of black chokeberry, *A. melanocarpa*, do to their similar fruit color. Common cultivars include ‘Viking’, ‘Nero’, and ‘Aron’ (Dirr, 2009). However, *A. mitschurinii* does possess some unique distinctions from *A. melanocarpa*. Skvortsov and Maitulina (1982) identified it as having fruits 1.5-2 times larger than *A. melanocarpa*, larger inflorescences, rounder, more homogenous leaf morphology, and a faster growth rate. Fruit morphology is also distinct. Skvortsov and Maitulina (1982) described fruits of *A. mitschurinii* as dull, globular, somewhat depressed at the apex, compared to wild *A. melanocarpa* fruits which are shiny and oval or pyriform in shape. *Aronia mitschurinii* has also been documented to be tetraploid and exhibit limited phenotypic variation (Skvortsov and Maitulina, 1982; Jeppsson, 1999; Persson-Hovmalm et al., 2004). Historically, *A. mitschurinii* has been grown throughout the former Soviet Union and Scandinavia as a commercial fruit crop, reaching a production of 17,800 ha by 1984 (Skvortsov et al., 1983; Kask, 1987).

Recently, scientific and commercial interest in *A. mitschurinii* has increased significantly as fruits have been found to contain exceedingly high levels of antioxidants (Kahkonen et al., 1999; Kahkonen et al., 2001; Zheng and Wang, 2003; Wu et al., 2004; Brand, 2010). Despite the attention, the development of the *A. mitschurinii* phenotype has remained ambiguous. Skvortsov et al. (1983) traced *A. mitschurinii*'s origins back to early 20<sup>th</sup> century Russia and the research facility of pomologist Ivan Michurin. Michurin's notes describe many successful hybridizations between *Aronia*, *Sorbus* and other members of the subtribe Pyrinae, Rosaceae (Michurin, 1948; 1949). The Pyrinae is a group in which wide hybridizations and allopolyploidy have been important factors in speciation (Campbell and Wright, 1996; Campbell et al., 2007; Dickinson and Campbell, 1991; Evans and Campbell 2002; Nelson-Jones et al, 2002; Phipps et al., 1991; Potter et al., 2007; Robertson et al., 1991; and Robertson et al., 2010).

Though literature sources attribute *A. mitschurinii* to Ivan Michurin's research, the genetic relationship between it and the three wild *Aronia* species, and various other members of the Pyrinae remains unknown. The goal of this study is to determine if *A. mitschurinii* is a naturally occurring form of *Aronia*, or is the product of intergeneric hybridization. To study the genetics of *A. mitschurinii*, the amplified fragment length polymorphic (AFLP) molecular marking technique (Vos et al., 1995) was chosen for its reproducibility (Jones et al., 1997) and ability to generate large numbers of markers across diverse taxa.



## Materials and Methods

### *Plant materials*

Germplasm used in AFLP analysis is listed in Table 1. Fourteen genotypes of *Aronia* were selected, including nine *A. melanocarpa*, two *A. prunifolia*, and two *A. arbutifolia*. Tetraploid *A. melanocarpa* accessions UC031 and PI603106 were selected specifically for fruit sizes comparable to *A. mitschurinii*. Four diploid (PI613016, UC007, UC009, and UC010) and two additional tetraploid accessions (PI545687 and PI618684) were selected to represent the geographical range of *A. melanocarpa*. *Aronia arbutifolia* accessions included the cultivar ‘Brilliantissima’ and PI578096. *Aronia prunifolia* genotypes (AMES27010 and PI603107) were identified using morphological characteristics including degree of pubescence, persistence of purple fruit color (not changing to black) and fruit ripening dates significantly later than that of *A. melanocarpa*. *Aronia mitschurinii* germplasm included cultivars ‘Nero’ and ‘Viking’.

The intergeneric, F<sub>1</sub> hybrid species  $\times$ *Sorbaronia dippelii*,  $\times$ *S. alpina*, and  $\times$ *S. fallax* were included as potential intermediate species between *A. mitschurinii* and its possible *Sorbus* ancestry. A hybrid between maternal *A. melanocarpa* and  $\times$ *S. sorbifolia* (from chapter 2) was also included. For simplicity, this accession is described as a second generation hybrid and labeled as  $\times$ *S. sorbifolia* F<sub>2</sub>. This accession is representative of a possible  $\times$ *Sorbaronia* backcross to *Aronia* that may have produced *A. mitschurinii*.  $\times$ *Sorbaronia* ‘Ivan’s Beauty’, also included in the analysis, is a cultivated hybrid between *S. aucuparia* and an unidentified black fruited *Aronia* species. This cultivar is triploid and of low fertility (Brand and Connolly, unpublished data).

Seven species of *Sorbus* were included covering four subgenera. *Sorbus aria* var. *salicifolia* and *S. torminalis* represent the *Aria* and *Torminaria* aggregates, are native to Europe and are simple-leaved tree species. *Sorbus aucuparia* and *S. americana* represent the compound leaved *Sorbus* species of shrubs and small trees from North American and Eurasia. The East Asian natives *S. alnifolia* and *S. yuana*, representing *Micromeles*, are simple leaved tree species. *Sorbus latifolia* is considered an allopolyploid containing genetic material from *S. aria* and *S. torminalis*. All *Sorbus* taxa were present at the time of this study in the living collections of the Arnold Arboretum of Harvard University, Boston, MA.

Species chosen from the broader Pyrinae included genera utilized in Michurin's research such as *Malus* and *Pyrus*. A diverse array of *Malus* species was selected including *M. baccata*, *M. domestica*, *M. hupehensis*, and *M. platycarpa*. Widely available *Pyrus communis* and *P. calleryana* were included. Additional genera that have taxonomic links to *Aronia* included in the study are *Amelanchier* and *Photinia*. The East Asian genera *Chaenomeles* and *Cydonia* were selected as out groups and are not known to hybridize with *Aronia*.

#### *DNA isolation*

DNA from approximately 0.5 g of newly emerged fresh or frozen (-80°C) leaf tissue was isolated using a modified CTAB procedure (Holvm, 1995). Leaf tissue was ground in liquid nitrogen then transferred to 15 ml conical polypropylene Falcon® tubes (BD Falcon, Franklin Lakes, NJ). Frozen tissue was suspended in three ml DNA extraction buffer containing one mg ml<sup>-1</sup> RNase and 2.1µl β-mercaptoethanol. Tubes

were mixed vigorously for one minute, and incubated for one hour in a 60°C water bath. Samples were mixed by inversion at 15 minute intervals. Samples were then centrifuged for five minutes at  $2500 \times g$  and the supernatant was transferred to new 15 ml tubes. Next, 24:1 (v/v) chloroform:isoamyl alcohol was added at a ratio of approximately 1:1 (v/v) to each sample and shaken for one minute. Tubes were centrifuged for 10 min at  $2500 \times g$  and the aqueous phase was transferred to a new tube. This process was repeated until little to no interphase was visible. DNA was precipitated using 2:1 (v/v) ice cold 100% ethanol (EtOH) and samples were centrifuged and rinsed twice in 70% EtOH. Pellets were dissolved in TE<sub>0.1</sub> buffer (pH 8.0) to achieve a concentration of approximately  $300 \text{ ng } \mu\text{l}^{-1}$  and stored at 4°C, or at -20°C for long term storage. All centrifugation was done at 4°C. DNA quantification and quality were assessed on a NanoDrop® ND-1000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and by observing the DNA run on a 1% agarose gel. Minimum thresholds for absorbance ratios were 1.9 (A260/A280) and 1.5 (A260/A230).

#### *AFLP analysis*

The AFLP procedure was utilized following the Applied Biosystems AFLP® plant mapping protocol (Applied Biosystems, Foster City, CA, USA). Restriction-ligation enzymes were purchased from New England Biolabs (Ipswich, MA, USA). Adaptor sequences, AFLP preselective primers and PCR amplification core mix were purchased from Applied Biosystems. Preselective primers had one selective nucleotide (*Eco*+A/*Mse*+C). Seven primer combinations were chosen for selective amplification (*Eco*+ACT/*Mse*+CAC, *Eco*+ACT/*Mse*+CTA, *Eco*+ACT/*Mse*+CAT,

*Eco*+ACT/*Mse*+CTG , *Eco*+AGG/*Mse*+CTC, *Eco*+AGG/*Mse*+CAT, *Eco*+AGG/*Mse*+CAC). Fluorescently labeled *Eco* RI and unlabeled *Mse* I primers were purchased from Applied Biosystems. Fragments produced for primer combinations *Eco*+ACT/*Mse*+CAC, *Eco*+ACT/*Mse*+CTA, *Eco*+ACT/*Mse*+CAT and *Eco*+AGG/*Mse*+CTC were separated using an Applied Biosystems ABI 3130x Genetic Analyzer. Fragments for primer combinations *Eco*+ACT/*Mse*+CTG, *Eco*+AGG/*Mse*+CAT and *Eco*+AGG/*Mse*+CAC were separated on an Applied Biosystems ABI 3730xl Genetic Analyzer at the Cornell University Life Sciences Core Laboratories Center (Ithaca, NY). Samples were prepared for analysis by mixing 1 µl selective PCR product with 9.85 µl deionised formamide containing 0.15 µl GeneScan® 500 [LIZ®](Applied Biosystems). To insure reproducibility, DNA for all individuals was isolated in duplicate and final AFLP fragment products were compared. Fragment data was scored using GeneMarker® version 1.95 software (Softgenetics, State College, PA, USA). Peaks were scored for products ranging in length from 75-500 base pairs for primer combinations *Eco*+ACT/*Mse*+CAC, *Eco*+ACT/*Mse*+CTA, *Eco*+ACT/*Mse*+CAT, and *Eco*+AGG/*Mse*+CTC. For primer combinations *Eco*+ACT/*Mse*+CTG, *Eco*+AGG/*Mse*+CAT, and *Eco*+AGG/*Mse*+CAC were scored from 60-300 base pairs. All peaks were confirmed visually before being exported as a binary matrix (present = 1, absent = 0).

#### *Data analysis*

Similarity matrices were constructed using the SIMQUAL function in NTSYSpc 2.21 software (Exeter Software, Setauket, NY, USA)(Rohlf, 2005).

Phenograms were constructed in NTSYSpc using an unweighted pair-group method with arithmetic averages (UPGMA) cluster analysis. Bootstrapping was performed using PAUP\*4.0 (Swofford, 2002) and Nei-Li distances with 2000 thousand replicates. Cophenetic correlation coefficients were calculated to test the goodness of fit using a two-way Mental test in the MXCOMP module of NTSYSpc 2.21 (Exeter Software, Setauket, New York). The DCENTER and EIGEN functions were used to perform the original principal coordinates analysis which served as inputs for the non-metric multidimensional scaling (nMDS) using MDSCALE (Kruskal, 1964ab). To test the goodness of fit between the original distances and fitted values the Stress1 coefficient was used. nMDS was run on up to five dimensions with the fifth (0.05) considered an excellent fit of the data (Kruskal, 1964ab). Additional simulations produced insignificant changes in stress values. Since more than two dimensions were chosen, a principal components analysis (PCA) was performed on the nMDS to line-up trends of variation in the configuration space with the coordinate axes. The first three dimensions explained 86.8% of the data.

To challenge similarity clustering, a Bayesian method was implemented using the program Structure 2.3.3 (Pritchard et al., 2000). Structure was developed as a population genetics tool to examine gene flow between groups or individuals. One drawback is that the software assumes equal ploidy levels across operational taxonomical units, which the taxa in this study do not have. To accommodate this, all individuals were treated as haploid. With dominant marking techniques, such as AFLP, this treatment has the tendency to distort the genetic distances, with offspring of ploidy mismatched parents reflecting greater similarity to one parent over another. However, as

the goal of this study is to merely identify hybridity, the distortions are acceptable. The web based program Harvester (Earl, 2009) was used to compute  $\Delta K$  values following Evanno et al. (2005). Structure was run for 10 iterations with a burn-in period of 5,000 cycles and sample of 25,000 in the Markov chain Monte Carlo simulations. Our analysis considered conceptual populations ( $K$ s) from 1 to 10.

## Results and Discussion

### *Distance analysis*

From the seven primer combinations 769 scorable bands were identified, 4 of which were monomorphic across all taxa. *Aronia* samples UC007 and PI578096 produced un-replicated profiles for primer combinations *Eco*+ACT/*Mse*+CTA and *Eco*+AGG/*Mse*+CTC respectively and were treated as missing data (0.7% of entire data set). Reproducibility of the DNA isolation and AFLP procedures was tested using clonal *S. aria* accessions, which produced identical profiles. *Aronia mitschurinii* cultivars ‘Viking’ and ‘Nero’ also produced identical fingerprints. Cophenetic correlation values for Jaccard’s and Dice similarity coefficients were compared with Jaccard’s producing the highest value (0.93). Pairwise similarities ranged from 0.149 to 0.876 for non-identical taxa, averaging 0.322 with a standard deviation of 0.140 (Table 2).

Pairwise cophenetic correlation coefficients observed for *Aronia mitschurinii* were highest between  $F_1$  hybrids  $\times S.$  ‘Ivan’s Beauty’ (0.675),  $\times S. fallax$  (0.612), and  $\times S. sorbifolia$   $F_2$  (0.608). Intergeneric generic hybrids involving *S. aria*, including  $\times S. alpina$ ,  $\times S. dippelii$ , had lower cophenetic correlation coefficients with *A. mitschurinii* (0.471, 0.502 and 0.471 respectively) than hybrids with *S. aucuparia*. Between *Sorbus*

species, *A. mitschurinii* also had higher similarity values when compared to *S. aucuparia* (0.459) and *S. americana* (0.411) than *S. aria* (0.236), *S. torminalis* (0.245) and *S. yuana* (0.256). In comparing *A. mitschurinii* to other *Aronia* species, mean similarity values for *A. melanocarpa* (0.535) and *A. prunifolia* (0.537) were higher than for *A. arbutifolia* (0.461). Amongst *Aronia*, *A. melanocarpa* UC010 was observed to have the greatest cophenetic correlation coefficient at (0.597).

The UPGMA tree (Figure 1) revealed three main groups. *Cydonia* clustered with *Chaenomeles* forming an out group with 75 percent bootstrap support. *Amelanchier*, *Photinia*, and a weakly supported *Malus/Pyrus* subgroup form a distinct cluster (group I). A second major group (group II) consists of *Sorbus*, *×Sorbaronia* and a modestly supported *Aronia* subgroup. Within this cluster, a branch consisting of *×S. fallax* and *A. mitschurinii* could be distinguished from the *Aronia* species with a bootstrap support of 66 percent.

Figure 2 is a two dimensional PCA plot derived from the nMDS ordination of taxa within group II. Though dimensions one and two account for a greater percentage of the data (74%), this analysis focuses on dimensions one and three (60.6%). It was observed that when the three-dimensional plot was reduced to two-dimensions for easier viewing, dimensions one and three were found to be more representative of the three-dimensional positioning between *Aronia* and *A. mitschurinii*. In figure 2, *Aronia* species formed a distinct cluster. *Aronia arbutifolia* could be distinguished from *A. melanocarpa*, however the two *A. prunifolia* accessions overlapped the other two groups. *Aronia melanocarpa* accession UC007 fell on a different plane in the three-dimensional plots though it appears to overlap with *A. arbutifolia* when viewed in two-dimensional

plots. This accession is a compact diploid collected in Connecticut. Simple and compound leaved *Sorbus* species did not cluster closely. Compound-leaved *S. americana* and *S. aucuparia* grouped closely, but the simple-leaved group was less cohesive. *Sorbus torminalis* did not cluster with any other *Sorbus* species. When observed in a three-dimensional model East Asian species formed a distinct cluster from European *Sorbus*.  $\times$ *Sorbaronia* genotypes could be identified falling intermediately between the parental species. *Aronia mitschurinii* cultivars ‘Nero’ and ‘Viking’ fell in between the *Aronia* cluster and  $\times$ *S. fallax*.  $\times$ *Sorbaronia sorbifolia* F<sub>2</sub>, the backcrossed  $\times$ *S. sorbifolia* to *A. melanocarpa*, appears in close proximity to *A. mitschurinii*.

#### *Bayesian analysis*

For the Bayesian analysis the total number of taxa was reduced to include only *Aronia melanocarpa*, *Sorbus aucuparia* and *S. americana*, and their intergeneric hybrids. A data set containing additional taxa proved unworkable for Structure, with the software unable to identify generic boundaries, or deceptively placed  $\times$ *Sorbaronia* individuals as standalone genotypes, unreflective of their hybridity. Following the methods of Evanno et al. (2005) it was determined that the data is best represented by 7 conceptual populations (Figures 3 and 4). However, the results presented in figure 5 focus on a *K* of 2 for a variety of reasons: (i) a secondary peak is observed at *K*=2, (ii) the variance of  $\ln(K)$  at *K*=2 is less than at *K*=7 and (iii) *K*=2 is consistent with the two genetic extremes of *Aronia melanocarpa* and *Sorbus aucuparia*/*S. americana*, allowing detection of intermediate species while excluding within species genetic variation.



In the  $K=2$  solution *Aronia melanocarpa* forms a distinct cluster, as does *Sorbus aucuparia* and *S. americana*. *Aronia mitschurinii* ‘Viking’ is observed to be split between the two genotypes as is the backcrossed  $\times$ *Sorbaronia sorbifolia* F<sub>2</sub>.  $\times$ *Sorbaronia fallax* and  $\times$ S. ‘Ivan’s Beauty’ did not separate from the *A. aucuparia* genotype.

## Conclusions

This study substantially improved the understanding of the relationship between *A. mitschurinii* and wild North American *Aronia*. Two groups with greater than 50% bootstrap support could be identified in Figure 1. Of the species with taxonomic links to *Aronia*, only *Sorbus* demonstrated a genetic similarity.  $\times$ *Sorbaronia fallax* and  $\times$ S. ‘Ivan’s Beauty’ combined with *A. mitschurinii* to form a moderately supported branch between the *Sorbus* and *Aronia* groups, suggesting that *A. mitschurinii* is a hybrid between *Aronia* and *Sorbus*. In addition, Figure 2 produced a clear genetic progression between *Aronia* and compound leaved *Sorbus* species. The close proximity of  $\times$ S. *sorbifolia* F<sub>2</sub> to *A. mitschurinii* in Figure 2, and its distance from wild North American *Aronia* supports Skvortsov et. al (1983)’s assertion that this species is the product of wide hybridization with *Sorbus* subgenus *Sorbus*. Results of the Bayesian analysis support distance methods. The Structure output presented in Figure 5 show a split in *A. mitschurinii*’s profile between the two extremes of *A. melanocarpa* and compound leaved *Sorbus*, characteristic of a hybrid species. A similar split is observed in the backcrossed accession  $\times$ S. *sorbifolia* F<sub>2</sub>.

Michurin’s notes do not mention crosses of *Aronia* with *S. americana* or that he recieved any wild  $\times$ *Sorbaronia* hybrids from North America (Michurin 1948, 1949).

Based on this, and the relative ease at which *S. aucuparia* hybridizes with *Aronia*, we are confident to implicate *S. aucuparia* as the source of *Sorbus* genetic material observed in *A. mitschurinii*. We are also confident *A. mitschurinii* is the product of  $\times S. fallax$  backcrossed to a black-fruited *Aronia* species. The belief that Michurin received a large fruited form of *A. melanocarpa* that subsequently was rebranded as *A. mitschurinii* is not supported by this data. Large-fruited accessions UC031 and PI603106 produced lower cophenetic correlation coefficients with *A. mitschurinii* than did *Aronia* accessions with average-sized fruits. It does seem likely that the *Aronia* parent was either *A. melanocarpa* or a dark fruited form of *A. prunifolia* as indicated by Michurin's notes specifying a "black-fruited" *Aronia*. Our data supports this showing higher pair-wise similarities between *A. mitschurinii* and dark-fruited *A. melanocarpa* and *A. prunifolia* than between *A. arbutifolia*. These species also share a number of morphological characteristics including black fruits and nearly glabrous leaves and stems. Though *Aronia mitschurinii* is presented as an intergeneric hybrid we do not propose nomenclatural changes to express *Sorbus* genetics. Since the data demonstrates *A. mitschurinii* to be backcrossed one or more times to *Aronia*, Skvortsov and Maitulina's (1982) treatment is adequate.

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**Table 2. Germplasm information for material used in AFLP analysis.**

Species	Accession/Cultivar	Germplasm/Hybrid Source	Germplasm Origin
<i>Amelanchier arborea</i>	-	Blue Ridge Hills Reservation, Milton, MA	Wild
<i>Amelanchier nantucketensis</i>	-	Blue Ridge Hills Reservation, Milton, MA	Wild
<i>Aronia arbutifolia</i>	'Brilliantissima'	Spring Meadow Nursery, Grand Haven, MI	Cultivated origin
<i>Aronia arbutifolia</i>	PI578096	USDA, Ames, IA	Virginia
<i>Aronia melanocarpa</i>	UC007	University of Connecticut, Storrs, CT	Halls pond, Chaplin, CT
<i>Aronia melanocarpa</i>	UC009	University of Connecticut, Storrs, CT	Damariscotta lake, Nobleboro, ME
<i>Aronia melanocarpa</i>	UC010	University of Connecticut, Storrs, CT	Damariscotta lake, Nobleboro, ME
<i>Aronia melanocarpa</i>	UC031	University of Connecticut, Storrs, CT	Windsor, CT
<i>Aronia melanocarpa</i>	PI545687	USDA, Ames, IA	Michigan
<i>Aronia melanocarpa</i>	PI603106	USDA, Ames, IA	Tennessee
<i>Aronia melanocarpa</i>	PI613016	USDA, Ames, IA	Massachusetts
<i>Aronia melanocarpa</i>	PI618684	USDA, Ames, IA	Wisconsin
<i>Aronia mitschurinii</i>	'Nero'	Spring Meadow Nursery, Grand Haven, MI	Cultivated origin
<i>Aronia mitschurinii</i>	'Viking'	Spring Meadow Nursery, Grand Haven, MI	Cultivated origin
<i>Aronia prunifolia</i>	AMES27010	USDA, Ames, IA	Michigan
<i>Aronia prunifolia</i>	PI603107	USDA, Ames, IA	Virginia
<i>Chaenomeles japonica</i>	750-82-A	Arnold Arboretum, Boston, MA	Cultivated origin
<i>Chaenomeles speciosa</i>	-	University of Connecticut, Storrs, CT	Landscape specimen of cultivated origin
<i>Cydonia oblonga</i>	829-84-A	Arnold Arboretum, Boston, MA	Forestry Sch., Loiret, France
<i>Malus baccata</i>	1843-80-A	Arnold Arboretum, Boston, MA	China
<i>Malus domestica</i>	'Cameo'	Wright Orchard, Willington, CT	Orchard specimen of cultivated origin
<i>Malus domestica</i>	'Macoun'	Wright Orchard, Willington, CT	Orchard specimen of cultivated origin
<i>Malus hupehensis</i>	21-96-C	Arnold Arboretum, Boston, MA	Cultivated origin
<i>Malus platycarpa</i>	134-2004-A	Arnold Arboretum, Boston, MA	Franklin, NC
<i>Photinia beauverdiana</i>	1733-80-A	Arnold Arboretum, Boston, MA	W. Hubei Shennongjia Forest District, China
<i>Photinia villosa</i>	-	University of Connecticut, Storrs, CT	Landscape specimen of cultivated origin
<i>Pyrus calleryana</i>	-	University of Connecticut, Storrs, CT	Landscape specimen of cultivated origin
<i>Pyrus communis</i>	'Bartlett'	Private residence	Orchard specimen of cultivated origin
<i>Sorbus alnifolia</i>	1497-52-B	Arnold Arboretum, Boston, MA	Royal Botanical Garden, Kew, England
<i>Sorbus americana</i>	1845-66-A	Arnold Arboretum, Boston, MA	Alberta, Canada
<i>Sorbus aria</i>	222-27-A	Arnold Arboretum, Boston, MA	Royal Botanical Garden, Edinburgh, Scotland
<i>Sorbus aria</i>	260-27-A	Arnold Arboretum, Boston, MA	Royal Botanical Garden, Edinburgh, Scotland
<i>Sorbus aucuparia</i>	180-57-A	Arnold Arboretum, Boston, MA	Hiller Nurseries, England
<i>Sorbus latifolia</i>	18462-B	Arnold Arboretum, Boston, MA	Vilmorin-Andrieux, France
<i>Sorbus torminalis</i>	183-2002-C	USDA, Ames, IA	Cultivated origin
<i>Sorbus yuana</i>	1539-80-C	Arnold Arboretum, Boston, MA	W. Hubei Shennongjia Forest District, China
× <i>Sorbaronia</i>	'Ivan's Beauty'	University of Connecticut, Storrs, CT	Cultivated origin
× <i>Sorbaronia alpina</i>	994-84-A	Arnold Arboretum, Boston, MA	Royal Botanical Garden, Kew, England
× <i>Sorbaronia dippelii</i> 1	759-78	Arnold Arboretum, Boston, MA	Simon-Louis Freres, Germany
× <i>Sorbaronia dippelii</i> 2	-	<i>A. melanocarpa</i> UC007 × <i>S. aria</i> 222-27-A	University of Connecticut, Storrs, CT
× <i>Sorbaronia fallax</i>	-	University of Connecticut, Storrs, CT	St. Dennis Cemetery, Kenton Rd, Ashburnham, MA
× <i>Sorbaronia sorbifolia</i> F <sub>2</sub>	UC120	<i>A. melanocarpa</i> UC007 × <i>S. sorbifolia</i> 1239-85-A*	University of Connecticut, Storrs, CT

\*×*Sorbaronia sorbifolia* 1239-85-A is in the living collections of the Arnold Arboretum, Boston, MA. Accession was collected as a feral hybrid in Nova Scotia, Canada.

**Table 2. Pairwise similarity matrix based on Jaccard's coefficient for taxa used in UPGMA clustering and nMDS plot.**

	<i>Sorbus aria</i> 222	<i>Sorbus aria</i> 260	<i>Aronia prunifolia</i> 27010	<i>Aronia melanocarpa</i> 545687	<i>Aronia arbutifolia</i> 578096	<i>Aronia arbutifolia</i> 603106
<i>Sorbus aria</i> 222	1.00	-	-	-	-	-
<i>Sorbus aria</i> 260	1.00	1.00	-	-	-	-
<i>Aronia prunifolia</i> 27010	0.244	0.244	1.00	-	-	-
<i>Aronia melanocarpa</i> 545687	0.254	0.254	0.701	1.00	-	-
<i>Aronia arbutifolia</i> 578096	0.197	0.197	0.667	0.577	1.00	-
<i>Aronia arbutifolia</i> 603106	0.246	0.246	0.638	0.661	0.567	1.00
<i>Aronia prunifolia</i> 603107	0.237	0.237	0.692	0.632	0.671	0.573
<i>Aronia melanocarpa</i> 613016	0.252	0.252	0.647	0.64	0.588	0.577
<i>Aronia melanocarpa</i> 618684	0.23	0.23	0.779	0.696	0.68	0.658
<i>Sorbus alnifolia</i>	0.362	0.362	0.226	0.241	0.221	0.258
× <i>Sorbaronia alpina</i>	0.527	0.527	0.478	0.5	0.432	0.456
<i>Sorbus americana</i>	0.267	0.267	0.316	0.328	0.309	0.353
× <i>Sorbaronia dippelii</i> 2	0.534	0.534	0.526	0.518	0.464	0.467
× <i>Sorbaronia sorbifolia</i> F <sub>2</sub>	0.233	0.233	0.547	0.498	0.519	0.5
<i>Amelanchier arborea</i>	0.262	0.262	0.221	0.222	0.191	0.223
<i>Sorbus aucuparia</i>	0.252	0.252	0.349	0.329	0.359	0.35
<i>Malus baccata</i>	0.268	0.268	0.243	0.234	0.23	0.24
<i>Photinia beauverdiana</i>	0.251	0.251	0.258	0.225	0.214	0.236
<i>Aronia arbutifolia</i> UC001	0.224	0.224	0.586	0.521	0.62	0.511
<i>Pyrus calleryana</i>	0.231	0.231	0.236	0.217	0.223	0.243
<i>Malus</i> 'Cameo'	0.263	0.263	0.264	0.249	0.277	0.261
<i>Pyrus communis</i>	0.237	0.237	0.226	0.203	0.223	0.243
× <i>Sorbaronia dippelii</i> 1	0.505	0.505	0.506	0.51	0.456	0.488
× <i>Sorbaronia fallax</i>	0.25	0.25	0.514	0.494	0.482	0.484
<i>Malus hupehensis</i>	0.251	0.251	0.239	0.221	0.239	0.232
× <i>Sorbaronia</i> 'Ivan's Beauty'	0.256	0.256	0.474	0.473	0.425	0.429
<i>Chaenomeles japonica</i>	0.214	0.214	0.235	0.235	0.215	0.217
<i>Sorbus latifolia</i>	0.594	0.594	0.233	0.242	0.215	0.239
<i>Malus</i> 'Macoun'	0.249	0.249	0.237	0.233	0.242	0.258
<i>Amelanchier nantucketensis</i>	0.256	0.256	0.199	0.213	0.193	0.206
<i>Aronia mitschurinii</i> 'Nero'	0.236	0.236	0.569	0.59	0.483	0.531
<i>Cydonia oblonga</i>	0.183	0.183	0.188	0.195	0.164	0.205
<i>Malus platycarpa</i>	0.252	0.252	0.215	0.236	0.203	0.229
<i>Chaenomeles speciosa</i>	0.204	0.204	0.211	0.203	0.203	0.19
<i>Sorbus torminalis</i>	0.318	0.318	0.259	0.254	0.249	0.276
<i>Aronia melanocarpa</i> UC009	0.231	0.231	0.652	0.587	0.57	0.563
<i>Aronia melanocarpa</i> UC007	0.254	0.254	0.556	0.5	0.5	0.469
<i>Aronia melanocarpa</i> UC010	0.241	0.241	0.668	0.621	0.569	0.567
<i>Aronia melanocarpa</i> UC031	0.214	0.214	0.643	0.603	0.593	0.586
<i>Aronia mitschurinii</i> 'Viking'	0.236	0.236	0.569	0.59	0.483	0.531
<i>Photinia villosa</i>	0.23	0.23	0.243	0.217	0.225	0.236
<i>Sorbus yuana</i>	0.379	0.379	0.252	0.261	0.220	0.268

Table 2. continued

	<i>Aronia prunifolia</i> 603107	<i>Aronia melanocarpa</i> 613016	<i>Aronia melanocarpa</i> 618684	<i>Sorbus alnifolia</i>	× <i>Sorbaronia alpina</i>	<i>Sorbus americana</i>
<i>Aronia prunifolia</i> 603107	1.00	-	-	-	-	-
<i>Aronia melanocarpa</i> 613016	0.564	1.00	-	-	-	-
<i>Aronia melanocarpa</i> 618684	0.629	0.653	1.00	-	-	-
<i>Sorbus alnifolia</i>	0.233	0.276	0.245	1.00	-	-
× <i>Sorbaronia alpina</i>	0.452	0.465	0.455	0.316	1.00	-
<i>Sorbus americana</i>	0.336	0.344	0.336	0.249	0.321	1.00
× <i>Sorbaronia dippelii</i> 2	0.475	0.508	0.489	0.292	0.661	0.347
× <i>Sorbaronia sorbifolia</i> F <sub>2</sub>	0.477	0.572	0.549	0.24	0.426	0.393
<i>Amelanchier arborea</i>	0.232	0.227	0.221	0.227	0.257	0.251
<i>Sorbus aucuparia</i>	0.332	0.365	0.343	0.266	0.317	0.613
<i>Malus baccata</i>	0.245	0.23	0.247	0.242	0.253	0.256
<i>Photinia beauverdiana</i>	0.255	0.241	0.229	0.226	0.244	0.231
<i>Aronia arbutifolia</i> UC001	0.638	0.498	0.594	0.256	0.408	0.249
<i>Pyrus calleryana</i>	0.243	0.232	0.235	0.233	0.251	0.244
<i>Malus</i> ‘Cameo’	0.275	0.257	0.271	0.266	0.281	0.267
<i>Pyrus communis</i>	0.209	0.254	0.231	0.257	0.241	0.254
× <i>Sorbaronia dippelii</i> 1	0.467	0.487	0.475	0.313	0.876	0.333
× <i>Sorbaronia fallax</i>	0.492	0.483	0.494	0.242	0.453	0.488
<i>Malus hupehensis</i>	0.255	0.236	0.243	0.242	0.248	0.241
× <i>Sorbaronia</i> ‘Ivan’s Beauty’	0.431	0.424	0.445	0.258	0.455	0.477
<i>Chaenomeles japonica</i>	0.232	0.259	0.23	0.209	0.226	0.202
<i>Sorbus latifolia</i>	0.235	0.221	0.229	0.365	0.444	0.273
<i>Malus</i> ‘Macoun’	0.262	0.249	0.25	0.251	0.238	0.259
<i>Amelanchier nantucketensis</i>	0.237	0.218	0.213	0.212	0.248	0.242
<i>Aronia mitschurinii</i> ‘Nero’	0.504	0.52	0.552	0.229	0.471	0.411
<i>Cydonia oblonga</i>	0.21	0.183	0.195	0.183	0.205	0.19
<i>Malus platycarpa</i>	0.205	0.215	0.211	0.254	0.245	0.256
<i>Chaenomeles speciosa</i>	0.209	0.217	0.216	0.205	0.204	0.208
<i>Sorbus torminalis</i>	0.266	0.242	0.253	0.29	0.307	0.345
<i>Aronia melanocarpa</i> UC009	0.557	0.645	0.599	0.238	0.434	0.372
<i>Aronia melanocarpa</i> UC007	0.5	0.599	0.569	0.258	0.407	0.281
<i>Aronia melanocarpa</i> UC010	0.575	0.636	0.619	0.237	0.445	0.337
<i>Aronia melanocarpa</i> UC031	0.574	0.621	0.699	0.238	0.45	0.322
<i>Aronia mitschurinii</i> ‘Viking’	0.504	0.52	0.552	0.229	0.471	0.411
<i>Photinia villosa</i>	0.24	0.24	0.233	0.236	0.256	0.236
<i>Sorbus yuana</i>	0.258	0.260	0.255	0.574	0.342	0.27



Table 2. continued

	× <i>Sorbaronia dippelii</i> 2	× <i>Sorbaronia sorbifolia</i> F <sub>2</sub>	<i>Amelanchier arborea</i>	<i>Sorbus aucuparia</i>	<i>Malus baccata</i>	<i>Photinia beauverdiana</i>
× <i>Sorbaronia dippelii</i> 2	1.00	-	-	-	-	-
× <i>Sorbaronia sorbifolia</i> F <sub>2</sub>	0.478	1.00	-	-	-	-
<i>Amelanchier arborea</i>	0.25	0.219	1.00	-	-	-
<i>Sorbus aucuparia</i>	0.333	0.425	0.236	1.00	-	-
<i>Malus baccata</i>	0.236	0.232	0.21	0.251	1.00	-
<i>Photinia beauverdiana</i>	0.264	0.223	0.225	0.24	0.228	1.00
<i>Aronia arbutifolia</i> UC001	0.404	0.466	0.221	0.274	0.273	0.238
<i>Pyrus calleryana</i>	0.234	0.239	0.237	0.267	0.284	0.219
<i>Malus</i> ‘Cameo’	0.255	0.243	0.231	0.252	0.431	0.251
<i>Pyrus communis</i>	0.239	0.234	0.211	0.278	0.29	0.242
× <i>Sorbaronia dippelii</i> 1	0.703	0.435	0.272	0.324	0.245	0.259
× <i>Sorbaronia fallax</i>	0.464	0.541	0.232	0.565	0.244	0.231
<i>Malus hupehensis</i>	0.246	0.233	0.216	0.256	0.686	0.215
× <i>Sorbaronia</i> ‘Ivan’s Beauty’	0.434	0.467	0.237	0.575	0.255	0.259
<i>Chaenomeles japonica</i>	0.228	0.244	0.21	0.214	0.207	0.247
<i>Sorbus latifolia</i>	0.422	0.214	0.216	0.249	0.274	0.248
<i>Malus</i> ‘Macoun’	0.253	0.236	0.214	0.238	0.397	0.232
<i>Amelanchier nantucketensis</i>	0.237	0.21	0.538	0.226	0.224	0.22
<i>Aronia mitschurinii</i> ‘Nero’	0.471	0.532	0.228	0.459	0.239	0.235
<i>Cydonia oblonga</i>	0.194	0.185	0.192	0.195	0.243	0.215
<i>Malus platycarpa</i>	0.251	0.213	0.219	0.242	0.383	0.213
<i>Chaenomeles speciosa</i>	0.202	0.229	0.196	0.226	0.219	0.214
<i>Sorbus torminalis</i>	0.304	0.243	0.241	0.275	0.251	0.229
<i>Aronia melanocarpa</i> UC009	0.486	0.649	0.204	0.377	0.22	0.235
<i>Aronia melanocarpa</i> UC007	0.453	0.53	0.237	0.296	0.249	0.215
<i>Aronia melanocarpa</i> UC010	0.519	0.608	0.221	0.382	0.22	0.225
<i>Aronia melanocarpa</i> UC031	0.467	0.549	0.223	0.333	0.222	0.218
<i>Aronia mitschurinii</i> ‘Viking’	0.471	0.532	0.228	0.459	0.239	0.235
<i>Photinia villosa</i>	0.262	0.223	0.244	0.266	0.234	0.515
<i>Sorbus yuana</i>	0.323	0.246	0.244	0.288	0.270	0.259

Table 2. continued

	<i>A. arbutifolia</i> UC001	<i>Pyrus calleryana</i>	<i>Malus</i> ‘Cameo’	<i>Pyrus communis</i>	× <i>Sorbaronia dippelii</i> 1	× <i>Sorbaronia fallax</i>
<i>Aronia arbutifolia</i> UC001	1.00	-	-	-	-	-
<i>Pyrus calleryana</i>	0.241	1.00	-	-	-	-
<i>Malus</i> ‘Cameo’	0.284	0.272	1.00	-	-	-
<i>Pyrus communis</i>	0.241	0.456	0.238	1.00	-	-
× <i>Sorbaronia dippelii</i> 1	0.428	0.248	0.284	0.253	1.00	-
× <i>Sorbaronia fallax</i>	0.446	0.252	0.273	0.247	0.468	1.00
<i>Malus hupehensis</i>	0.263	0.265	0.427	0.288	0.246	0.24
× <i>Sorbaronia</i> ‘Ivan’s Beauty’	0.414	0.268	0.265	0.268	0.469	0.671
<i>Chaenomeles japonica</i>	0.24	0.22	0.184	0.22	0.247	0.213
<i>Sorbus latifolia</i>	0.233	0.251	0.259	0.23	0.414	0.243
<i>Malus</i> ‘Macoun’	0.251	0.251	0.682	0.24	0.248	0.252
<i>Amelanchier nantucketensis</i>	0.239	0.205	0.251	0.226	0.254	0.232
<i>Aronia mitschurinii</i> ‘Nero’	0.438	0.232	0.253	0.237	0.502	0.612
<i>Cydonia oblonga</i>	0.211	0.234	0.233	0.211	0.198	0.201
<i>Malus platycarpa</i>	0.206	0.238	0.436	0.219	0.242	0.229
<i>Chaenomeles speciosa</i>	0.215	0.197	0.185	0.204	0.206	0.204
<i>Sorbus torminalis</i>	0.249	0.261	0.263	0.249	0.295	0.264
<i>Aronia melanocarpa</i> UC009	0.468	0.237	0.251	0.227	0.46	0.504
<i>Aronia melanocarpa</i> UC007	0.517	0.217	0.235	0.24	0.432	0.447
<i>Aronia melanocarpa</i> UC010	0.476	0.248	0.246	0.232	0.473	0.553
<i>Aronia melanocarpa</i> UC031	0.521	0.218	0.25	0.219	0.475	0.477
<i>Aronia mitschurinii</i> ‘Viking’	0.438	0.232	0.253	0.237	0.502	0.612
<i>Photinia villosa</i>	0.247	0.225	0.265	0.247	0.271	0.239
<i>Sorbus yuana</i>	0.276	0.236	0.266	0.263	0.34	0.28

Table 2. continued

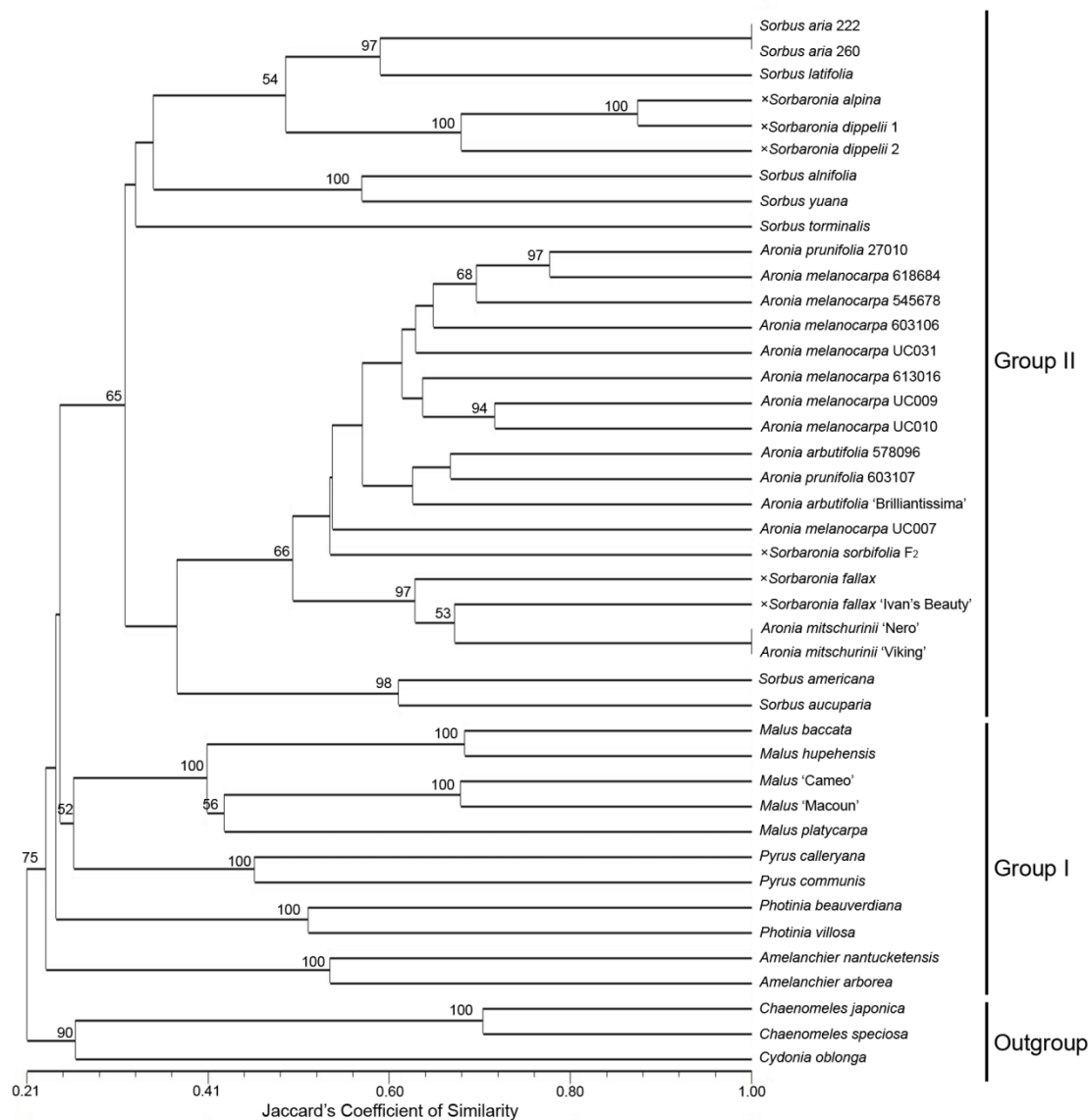
	<i>Malus hupehensis</i>	× <i>Sorbaronia</i> ‘Ivan’s Beauty’	<i>Chaenomeles japonica</i>	<i>Sorbus latifolia</i>	<i>Malus</i> ‘Macoun’	<i>Amelanchier</i> <i>nantucketensis</i>
<i>Malus hupehensis</i>	1.00	-	-	-	-	-
×S ‘Ivan’s Beauty’	0.255	1.00	-	-	-	-
<i>Chaenomeles japonica</i>	0.189	0.223	1.00	-	-	-
<i>Sorbus latifolia</i>	0.263	0.266	0.214	1.00	-	-
<i>Malus</i> ‘Macoun’	0.428	0.253	0.157	0.227	1.00	-
<i>Amelanchier nantucketensis</i>	0.25	0.228	0.195	0.211	0.243	1.00
<i>Aronia mitschurinii</i> ‘Nero’	0.244	0.675	0.227	0.243	0.238	0.224
<i>Cydonia oblonga</i>	0.227	0.202	0.239	0.201	0.209	0.202
<i>Malus platycarpa</i>	0.36	0.255	0.189	0.254	0.411	0.219
<i>Chaenomeles speciosa</i>	0.205	0.205	0.706	0.205	0.149	0.201
<i>Sorbus torminalis</i>	0.235	0.27	0.219	0.478	0.233	0.22
<i>Aronia melanocarpa</i> UC009	0.222	0.452	0.242	0.221	0.243	0.191
<i>Aronia melanocarpa</i> UC007	0.237	0.388	0.247	0.212	0.223	0.243
<i>Aronia melanocarpa</i> UC010	0.212	0.489	0.247	0.22	0.228	0.212
<i>Aronia melanocarpa</i> UC031	0.232	0.44	0.204	0.218	0.247	0.207
<i>Aronia mitschurinii</i> ‘Viking’	0.244	0.675	0.227	0.243	0.238	0.224
<i>Photinia villosa</i>	0.23	0.276	0.214	0.266	0.257	0.254
<i>Sorbus yuana</i>	0.264	0.286	0.203	0.374	0.247	0.255

Table 2. continued

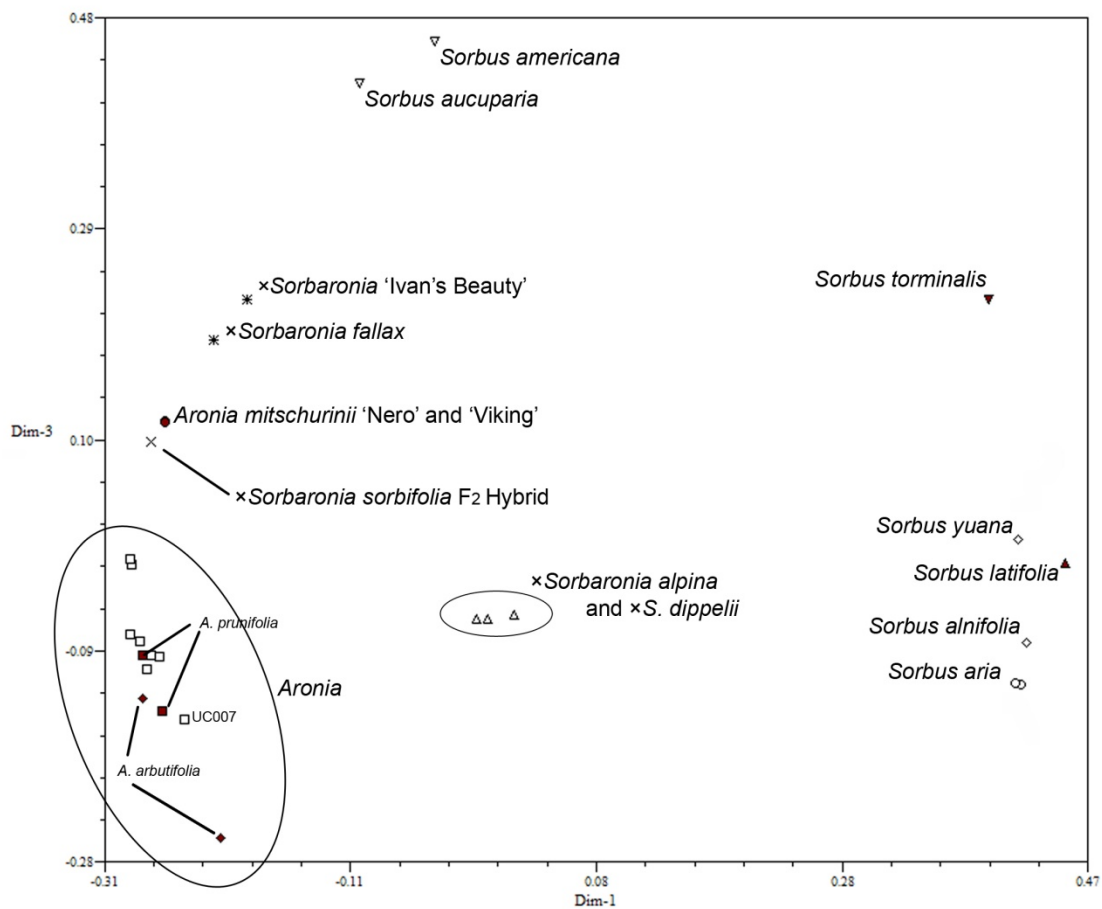
	<i>Aronia mitschurinii</i> ‘Nero’	<i>Cydonia oblonga</i>	<i>Malus platycarpa</i>	<i>Chaenomeles speciosa</i>	<i>Sorbus torminalis</i>	<i>Aronia melanocarpa</i> UC009
<i>Aronia mitschurinii</i> ‘Nero’	1.00	-	-	-	-	-
<i>Cydonia oblonga</i>	0.178	1.00	-	-	-	-
<i>Malus platycarpa</i>	0.237	0.2	1.00	-	-	-
<i>Chaenomeles speciosa</i>	0.198	0.282	0.181	1.00	-	-
<i>Sorbus torminalis</i>	0.245	0.216	0.247	0.214	1.00	-
<i>Aronia melanocarpa</i> UC009	0.54	0.184	0.224	0.212	0.256	1.00
<i>Aronia melanocarpa</i> UC007	0.46	0.176	0.206	0.228	0.237	0.571
<i>Aronia melanocarpa</i> UC010	0.597	0.172	0.201	0.201	0.241	0.719
<i>Aronia melanocarpa</i> UC031	0.551	0.158	0.201	0.192	0.25	0.641
<i>Aronia mitschurinii</i> ‘Viking’	1.00	0.178	0.237	0.198	0.245	0.54
<i>Photinia villosa</i>	0.243	0.221	0.241	0.2	0.25	0.24
<i>Sorbus yuana</i>	0.256	0.216	0.274	0.204	0.300	0.244

Table 2. continued

	<i>Aronia melanocarpa</i> UC007	<i>Aronia melanocarpa</i> UC010	<i>Aronia melanocarpa</i> UC031	<i>Aronia mitschurinii</i> ‘Viking’	<i>Photinia villosa</i>	<i>Sorbus yuana</i>
<i>Aronia melanocarpa</i> UC007	1.00	-	-	-	-	-
<i>Aronia melanocarpa</i> UC010	0.64	1.00	-	-	-	-
<i>Aronia melanocarpa</i> UC031	0.533	0.604	1.00	-	-	-
<i>Aronia mitschurinii</i> ‘Viking’	0.46	0.597	0.551	1.00	-	-
<i>Photinia villosa</i>	0.211	0.235	0.231	0.243	1.00	-
<i>Sorbus yuana</i>	0.249	0.254	0.239	0.256	0.248	1.00



**Figure 1. Phenogram created using the unweighted pair group method with arithmetic averages (UPGMA) based on Jaccard's coefficient of similarity for 42 members of Pyrinae. Bootstrap values of  $\geq 50\%$  are indicated to the left of each node.**



**Figure 2.** Principal components analysis (PCA) scatter plot derived from nonmetric multidimensional scaling (nMDS) of group II (figure 1). Displayed are dimensions one and three accounting for 60.6% of variation.

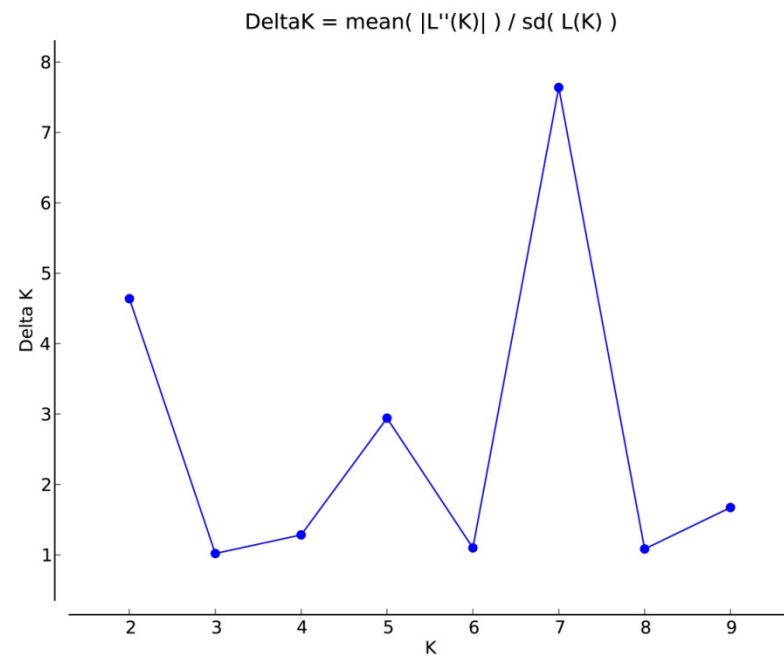


Figure 3.  $\Delta K$ , the second order increase in likelihood, for each conceptual population ( $K$ ) following Evanno et al. (2005).

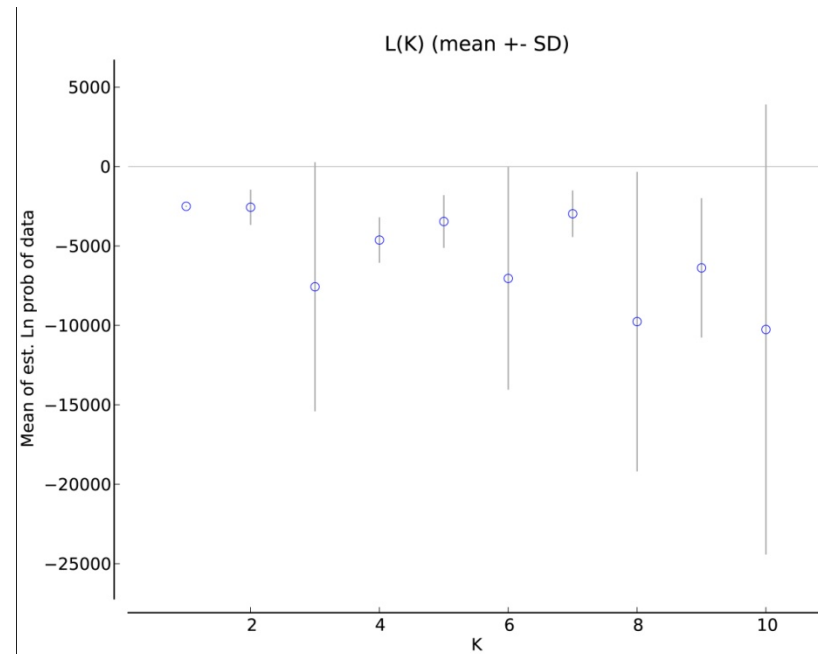


Figure 4. The average log likelihood of the 10 Structure iterations for each conceptual population ( $K$ ) following Pritchard et al. (2000).

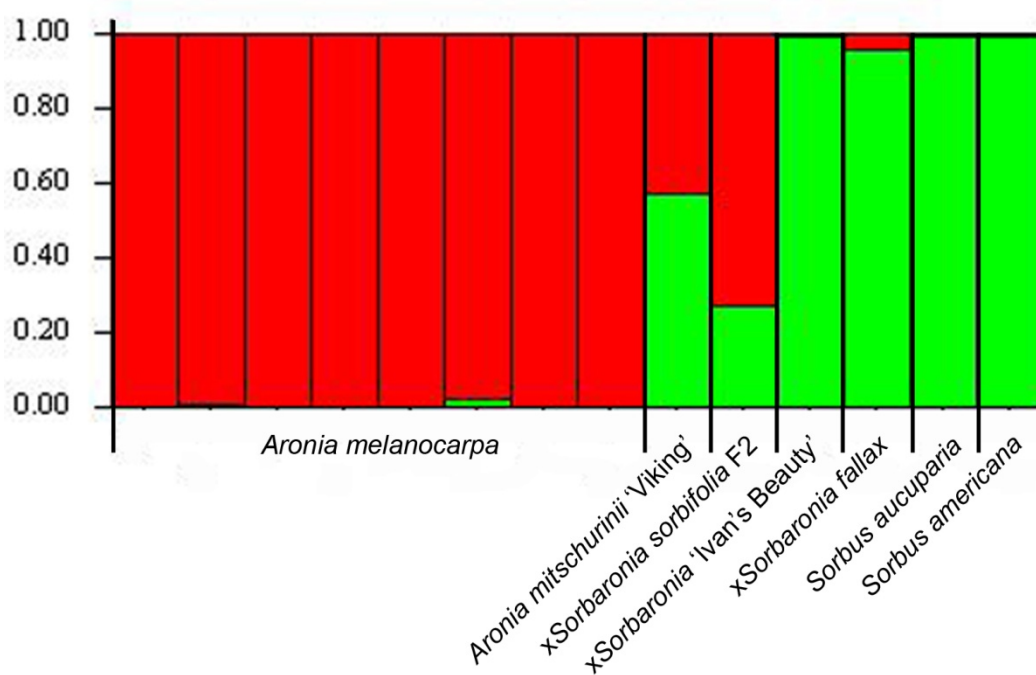


Figure 5. Bayesian analysis bar chart of eight wild North American *Aronia melanocarpa* accessions, *Aronia mitschurinii* 'Viking', three *xSorbaronia*, and *Sorbus* species *S. aucuparia* and *S. americana*. Red and green colors identify *A. melanocarpa* and *Sorbus* genetic influences respectively.