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RESEARCH ARTICLE

The vulnerability of US apple (*Malus*) genetic resources

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Abstract Apple (*Malus* × *domestica* Borkh.) is one of the top three US fruit crops in production and value. Apple production has high costs for land, labor and inputs, and orchards are a long-term commitment. Production is dominated by only a few apple scion and rootstock cultivars, which increases its susceptibility to dynamic external threats. Apple crop wild relatives, including progenitor species *Malus sieversii* (Ledeb.) M. Roem., *Malus orientalis* Uglitzk., *Malus sylvestris* (L.) Mill., and *Malus prunifolia* (Willd.) Borkh., as well as many other readily hybridized species, have a wide range of biotic and abiotic stress resistances as well as desirable productivity and fruit quality attributes. However, access to wild materials is limited and wild *Malus* throughout the world is at risk of loss due to human encroachment and changing climatic patterns. The USDA-ARS National Plant Germplasm System (NPGS) *Malus* collection, maintained by the Plant Genetic Resources Unit in Geneva, NY, US is among the largest collections of cultivated apple and *Malus* species in the world. The collection currently has 5004 unique accessions in the field and 1603 seed accessions representing *M.* × *domestica*, 33 *Malus* species, and 15 hybrid species. Of the trees in the field, 3,070 are grafted and are represented by a core collection of 258 individuals. Many wild species

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accessions are represented as single seedlings (non-grafted). The crop vulnerability status of apple in the US is moderate because although there are a few breeders developing new commercial cultivars who also access *Malus* species, threats and challenges include new diseases, pests, and changing climate combined with industry needs and consumer demands, with a limited number of cultivars in production.

Keywords Breeding · Disease resistance · Genetic diversity · Germplasm collections · *Malus* · Wild species

Introduction to *Malus*

Fruit from *Malus* × *domestica* Borkh. is consumed fresh, processed, and as juice. According to the Food and Agriculture Organization of the United Nations, apple production is ranked 17th in production value for agricultural products in both the US and world, with an annual crop value of more $31 billion worldwide (Online Resource 1). In 2008, there were approximately 7500 US commercial growers (U.S. International Trade Commission 2010). Among fruit and nut crops worldwide, apple production value ranked only below grape (Food and Agriculture Organization of the United Nations 2013).

According to the USDA National Agricultural Statistics Service (2014), the US fresh market apple crop was valued at $2.5 billion in 2011, with production of around 6.3 billion pounds of fruit. Processed apples (mostly juice and canned), composed about one third of the US apple crop. Processed fruit values were $341 million in 2011 for 3 billion pounds of fruit (USDA National Agricultural Statistics Service 2014). In the US, the total apple consumption in 2008 was 21 kg per capita, with 14 kg of that in the form of juice and cider (Economic Research Service 2012). For fresh fruit in 2007, Americans consumed about 7.5 kg of fresh apples per capita, while Turkish citizens consumed about 32 kg per capita and residents of Italy, New Zealand, Belgium, Germany, and France consumed more than 14 kg per capita (U.S. International Trade Commission 2010) (Online Resource 2).

The hard cider industry in the US is burgeoning, with sales of alcoholic cider tripling between 2007 and 2012, currently at about $600 million (Furnari 2013). In 2011, Vermont was the primary hard cider-producing state in the US. The United Kingdom has had the largest world-share of hard cider for decades, and cider composes 6 % of the UK alcoholic drink market. If the US follows the same trend, the hard cider industry will become an increasingly large market for apples.

Virtually all apple trees planted in commercial orchards were first produced in a nursery by grafting or budding the scion cultivar onto a rootstock. Rootstock cultivars are also classified as *M.* × *domestica*. Apple rootstocks are produced by layering or stooling propagation beds, which come in full production within 2 years of planting and have a production life span of 15–25 years. US apple rootstock nurseries annually produce between 15 and 19 million rootstock liners which are sold or transferred to finished tree nurseries and when combined with imported rootstocks from Europe result in the annual production of 17–21 million trees (average cost of $7 per tree) for a combined farm gate value of $120 million.

Crabapples are typically derived from one or more wild species. Crabapples are a steadfast component of the landscape industry and are the most widely cultivated small landscape tree in the US and Canada (Romer et al. 2003). Crabapple trees usually have fruit less than 5 cm in diameter. They are valued for their year-round ornamental attributes such as prolific flowering, attractive summer foliage, fall fruit color, winter bark coloration and fruit retention for wildlife (Klett and Cox 2008). Crabapple blossom colors range from white to deep red. Tree architecture can be weeping, rounded, spreading, upright, vase-shaped, or pyramidal (Fiala 1994).

Dietary contribution

Apples are an important contributor to human health as a valuable source of antioxidants and fiber. They are low-fat, low calorie and low in cholesterol and sodium. While apples are in ample supply in the US, not all individuals have access to high quality fruit (Othman et al. 2013). Apples tend to be absent in inner-city “food deserts”, yet studies indicate how this might be changed (Weatherspoon et al. 2013). Long-distance transport of apples is feasible, yet distances are a concern for those who consider food miles or carbon footprints in their food consumption habits (Blanke and Burdick 2005; Van Passel 2013).

Many studies have demonstrated the beneficial effects of consuming apples, with benefits ascribed to antioxidants, also known as polyphenols (Espley and Martens 2013). The levels of total polyphenols in apple are 5,230–27,240 mg/kg dw in whole apples and 110–970 mg/L in juice (Hyson 2011). Studies suggest that consuming one or more medium-sized apples per day was associated with a reduction in the risk of cancer and Parkinson's disease compared to consumption of fewer apples (Hyson 2011; Kukull 2012). Apple consumption has been shown to lead to reduced coronary mortality for both women and men and a reduced risk of asthma and related symptoms (Hyson 2011). Apple consumption may also reduce the risk of diabetes (Hyson 2011). Studies have also revealed that polyphenols in apple peels have beneficial actions on oxidative stress and inflammation (Denis et al. 2013). Apple juice consumption reduced accumulation of reactive oxygen species in brain tissue and attenuated cognitive impairment.

Apple fruit production

Cultivated apple trees are perennial and are composed of a scion and a rootstock that are vegetatively propagated and joined together by grafting. Scions are the aerial parts of the tree responsible for photosynthesis and bearing fruit, whereas rootstocks support scions by providing anchorage and enhancing uptake of soil nutrients and water. Rootstocks impart a particular level of dwarfing, productivity, and disease resistance to the scion, making them an integral part of apple production systems. Dwarfing rootstocks can decrease the size of a grafted scion by 90 %, compared to trees grown on their own roots or on non-dwarfing seedling rootstocks.

Flowers are highly susceptible to freezing temperatures and infection by critical production-threatening diseases (such as fire blight, *Erwinia amylovora* Burrill, and apple scab, *Venturia inaequalis* (Cooke) Wint.) may occur. The time of flowering and vegetative flushing is dependent upon the cultivar and orchard location. Apple trees have gametophytic self-incompatibility, where pollen must have at least one self-incompatibility allele that is different than the mother tree for fertilization and fruit set to occur (Hegedus 2006; Li et al. 2012a). Pollen, provided by purposefully planted pollinizer trees within the orchard, is spread by bees to the production trees. Due to recent declines in honeybee populations, the cost of pollinating orchards has increased (U.S. International Trade Commission 2010). Pollinizer trees must flower prolifically and at the same time as the production trees for successful pollination. Following successful pollination and fertilization, bloom-thinning methods such as chemical sprays or mechanical shaking may be applied to achieve durable final crop loads.

The apple harvest season in the US lasts from August to October. Harvested fruit is transported from the orchard to packers, who distribute fruit to retailers and exporters. Fruit are either distributed immediately to markets or placed into regular or controlled-atmosphere storage to extend the market life to year-round (Thompson 2010). Fruit are also imported from the southern hemisphere during late-spring and summer to help ensure year-round availability of apple fruit in the northern hemisphere (Canals et al. 2007).

Domestic and international crop production

Apples are a significant import and export crop for the US. In 2011, the US exported more than 820,000 MT of fresh apples to Mexico, Canada, India, Taiwan, and Hong Kong. Apple fruit export was valued at $941 million (Foreign Agricultural Service 2013). In addition, more than 34,000 kL of apple juice was exported to Canada, Japan, and Mexico, with a value of $34.7 million (Foreign Agricultural Service 2013). Due to the seasonality of apple availability, the US imports 147,790 MT of apples, with Chile its leading supplier. A total of 1.9 kL of juice valued at $715 million was imported in 2011 from China, Argentina, Chile, and Brazil. Apple juice imports from China have increased from 10 to 60 % of the US juice consumption, although it has been impacted by import duties.

US production

The state of Washington is the primary producer of apples in the US, with over 5,550 million pounds produced in 2010 and 60 % of the US apple production. Other significant production states include, in order of importance, New York, Michigan, Pennsylvania, Oregon, California, and Virginia, with more than 100 million pounds of apples each in 2010 (Economic Research Service 2012).

The number of commercial apple bearing acres in the US has dropped from about 390,000 acres in 2003 to less than 345,000 acres in 2010 (USDA Economic Research Service 2013). Despite this decline, production increased to more than 4,000,000 tons, largely due to the increased yields from high-density plantings (USDA, National Agricultural Statistics Service 2012). Organic apple exports ($100 million) accounted for nearly all of the growth in the organic export market in 2012 (Foreign Agricultural Service 2013).

International production

China produces the most apples worldwide, with a production value of more than $15 billion and more than 35 MT of fruit. The US is the second highest producer, with a production value of $1.8 billion and 4.2 MT of fruit in 2011 (Online Resource 3) (Food and Agriculture Organizations of the United Nations 2013). Other high-producing countries include India, Turkey, Poland, Italy, France, Iran, and the Russian Federation in the northern hemisphere and Brazil, Chile, and Argentina in the southern hemisphere (Online Resource 3) (Food and Agriculture Organizations of the United Nations 2013).

Production and demand

In the US, labor is the largest expense in the production of apples, accounting for about 42 % of production expenses (Calvin and Martin 2013) and US apple producers face production/demand competition from foreign producers with lower labor and land costs. Apples also require resources (e.g. water, fertile land) that are becoming increasingly scarce or unavailable because of urban sprawl and environmental regulations. In addition, food safety issues are always at the forefront for producers, as are immigration policy (picking crews), and export/import tariffs and sanitary and phytosanitary measures (U.S. International Trade Commission 2010).

Ecogeographical distribution

The taxonomy of *Malus* is not completely resolved; there are approximately 38 wild *Malus* species, and an additional 21 species and hybrids are only found under cultivated conditions (Table 1). Wild *Malus* species are found in East Asia, Southeast Asia, Central Asia, Southern Europe, and North America, and the center of diversity is located in China. Depending on species, they originate from both temperate and subtropical countries. A recent examination of genetic relationships among species using chloroplast DNA sequencing suggests that wild apple species fall into genetically distinct primary groups centered in China, Southeast Asia, Southern Europe, and North America (Nikiforova et al. 2013). Genetic relationships among wild species are not fully understood, although one North American species, *Malus fusca* (Raf.) C. K. Schneid., appears to be more closely related to several Chinese species than the other three North American species (*Malus angustifolia* (Aiton) Michx., *Malus coronaria* (L.) Mill., and *Malus ioensis* (Alph. Wood) Britton.

Germplasm base of US apple cultivation

The progenitor species of the domesticated apple is thought to be primarily *Malus sieversii* (Ledeb.) M. Roem. (from Central Asia) with likely contributions from *Malus sylvestris* (L.) Mill. (from Europe), *Malus orientalis* Uglitzk. (from the Mediterranean region), and *Malus prunifolia* (Willd.) Borkh (from China) (Cornille et al. 2012; Gross et al. 2012; Harris et al. 2002; Nikiforova et al. 2013; Velasco et al. 2010). Because *M. sieversii* exhibits many of the fruit attributes of *M.* × *domestica* (palatable flavor, large size, etc.), *M. sieversii* may have been an original progenitor, which was then introgressed with alleles from *M. orientalis* and *M. sylvestris* during the progression of the species (either by animals or by humans) from Central Asia to Europe (Hokanson et al. 1997). More recent introgressions by *M. sylvestris* may have occurred in some lineages, resulting in some close genetic relationships between *M. sylvestris* and *M.* × *domestica*. In Europe, apple clonal lineages were established and propagated for centuries, with gardeners and horticulturalists making crosses or simply cultivating volunteer seedlings and selecting among trees for new, desirable apple types to commercialize as cultivars for hard cider and fresh fruit consumption (Juniper and Mabberley 2006). Europe thereby became the primary center of diversity for *M.* × *domestica*.

Beginning in the 1700s, apple seeds were brought by settlers to North America as part of the European migration to the Americas (Juniper and Mabberley 2006). Seeds that survived the transatlantic passage

Table 1 Apple species and hybrids in the USDA-ARS National Plant Germplasm System *Malus* collection maintained by the Plant Genetic Resources Unit (PGRU) in Geneva, NY

Malus species or hybrid	Common name	Origin	Hybrid parentage	Resistance to pests and diseases	Abiotic stress resistance	Physiology	NPGs seed accessions	NPGS unique field trees	Primary ploidy	References
M. angustifolia (Aiton) Michx.	Southern crab	United States					40	19	2×, 3×, 4×	
M. baccata (L.) Borkh.	Siberian crab	Russia, China, Korea, India, Nepal		Apple scab, Bot canker, Fire blight, Powdery mildew	Cold hardiness, Waterlogging	Rootstock	17	50	2×	Luby et al. (2002), Le Roux et al. (2012), Dunemann and Schuster (2009), Yang et al. (2011), Hokanson et al. (2001), Wan et al. (2011), Zhi-Qin (1999), USDA (2014)
M. baoshanensis G. T. Deng		China					0	0		
M. brevipes (Rehder) Rehder		Cultivated					0	0	2×	
M. chitralensis Vassilcz.		Pakistan					0	0		
M. coronaria (L.) Mill.	Sweet crab apple	Northern America					48	50	2×, 3×, 4×	
M. crescimannoi Raimondo		Italy, Sicily					0	0		
M. doumeri (Bois) A. Chev.		China, Taiwan, Laos, Vietnam				Rootstock	1	1		USDA (2014)
M. florentina (Zuccagni) C. K. Schneid.	Hawthorn-leaf crab	Turkey, Albania, Greece, Italy, Macedonia, Serbia					0	3	2×	
M. floribunda Siebold ex Van Houtte	Japanese crab	Cultivated		Apple scab, Fire blight, Powdery mildew			1	11	2×	Le Roux et al. (2012), Fischer and Fischer (1999)
M. fusca (Raf.) C. K. Schneid.	Oregon crab	Northern America		Fire blight		Rootstock	190	41	2×	Le Roux et al. (2012), Flachowsky et al. (2011), Fischer and Fischer (1999), USDA (2014)

Table 1 continued

Malus species or hybrid	Common name	Origin	Hybrid parentage	Resistance to pests and diseases	Abiotic stress resistance	Physiology	NPGs seed accessions	NPGS unique field trees	Primary ploidy	References
M. halliana Koehne	Hall crab	China, cultivated			Waterlogging	Rootstock	0	15	2×, 3×, 4×	USDA (2014)
M. honanensis Rehder		China				Rootstock	1	3	2×	USDA (2014)
M. hupehensis (Pamp.) Rehder	Chinese crab	China, Taiwan		Powdery mildew	Drought, Flooding	Rootstock	22	142	3×	Yu (1979), Zhi-Qun (1999), Chen et al. (2012), Zhang et al. (2012a, b), Shi et al. (2012), USDA (2014)
M. ioensis (Alph. Wood) Britton	Iowa crab	United States					32	41	2×, 3×, 4×	
M. jinxianensis J. Q. Deng et J. Y. Hong							0	0		
M. kansuensis (Batalin) C. K. Schneid.		China		Apple scab	Cold hardiness, Drought		12	28	2×	Zhi-Qin (1999)
M. komarovii (Sarg.) Rehder		China, North Korea			Cold hardiness		1	1		
M. leiocalyca S. Z. Huang		China					0	0		
M. maerkangensis M. H. Cheng et al.		China					0	0		
M. mandshurica (Maxim.) Kom. ex Skvortsov	Manchurian crab	Russia, China, Japan, Korea			Cold hardiness	Rootstock	0	3	2×	Zhi-Qin (1999), USDA (2014)
M. muliensis T. C. Ku		China					0	0		
M. ombrophila Hand.-Mazz.		China					2	3	2×	
M. orientalis Uglitzk.		Iran, Turkey, Caucasus		Apple scab, Cedar apple rust, Fire blight			109	725	2×	Volk et al. (2005, 2008a)
M. orthocarpa Lavallee		Cultivated					0	1	2×	
M. pumila Mill.							1	12	2×	
M. prattii (Hemsl.) C. K. Schneid.		China					18	18	2×	

Table 1 continued

Malus species or hybrid	Common name	Origin	Hybrid parentage	Resistance to pests and diseases	Abiotic stress resistance	Physiology	NPGs seed accessions	NPGS unique field trees	Primary ploidy	References
M. prunifolia (Willd.) Borkh.	Chinese crab	China, cultivated		Apple scab, Bot canker, Fire blight	Cold hardiness	Rootstock	15	37	2×	Le Roux et al. (2012), Fischer and Fischer (1999), Hokanson et al. (2001), Zhi-Qin (1999), Wan et al. (2011), USDA (2014)
M. rockii Rehder				Powdery mildew	Water logging		0	0		Zhi-Qin (1999)
M. sargentii Rehder	Sargent's crab	Cultivated		Powdery mildew		Rootstock	2	21	3×, 4×, 5×	USDA (2014)
M. sieversii (Ledeb.) M. Roem.		China, Middle Asia		Apple scab, Bot canker, Fire blight, Powdery mildew, Blue mold	Cold hardiness, Water use efficiency, Drought	Rootstock, Red flesh	976	(1607)	2×	Kumar et al. (2010), Luby et al. (2002), Bassett et al. (2011), Zhi-Qin (1999), Luby et al. (2001), Hokanson et al. (2001), Norelli (2013), USDA (2014)
M. sikkimensis (Wenz.) Koehne ex C. K. Schneid.		China, Bhutan, India, Nepal		Powdery mildew		Rootstock	0	13	3×, 4×	Zhi-Qin (1999), USDA (2014)
M. spectabilis (Aiton) Borkh.	Asiatic apple	China, cultivated					1	9	2×, 3×	
M. spontanea (Makino) Makino		Japan					9	0		
M. sylvestris (L.) Mill.	European crab	Europe, cultivated		Blue mold		Rootstock	22	62	2×	USDA (2014), Jurick et al. (2011)
M. toringo Siebold (syn. *M. sieboldii* (Regel) Rehder ex Sargent)	Toringo crab	China, Japan, Korea, cultivated		Crown gall, Fire blight, Powdery mildew	Drought	Rootstock	34	83	3×	Moriya et al. (2010), Le Roux et al. (2012), Zhi-Qin (1999), USDA (2014)
M. toringoides (Rehder) Hughes, nom. cons. (syn. *M. bhutanica* (W.W. Sm.) Phipps)				Fire blight	Drought	Rootstock	6	89	2×, 3×	Zhi-Qun (1999), Luby et al. (2002), USDA (2014)
M. transitoria (Batalin) C. K. Schneid.		China			Cold hardiness, Drought	Rootstock	9	42	2×	Zhi-Qin (1999), USDA (2014)
M. trilobata (Poir.) C. K. Schneid.		Israel, Lebanon, Turkey, Bulgaria, Greece					0	0		

Table 1 continued

Malus species or hybrid	Common name	Origin	Hybrid parentage	Resistance to pests and diseases	Abiotic stress resistance	Physiology	NPGs seed accessions	NPGS unique field trees	Primary ploidy	References
M. tschonoskii C. K. Schneid.	Pillar apple	Japan, cultivated					0	3	2×	
M. × *adstringens* Zabel		Cultivated	*M. baccata* × *M. pumila*				0	2	2×	
M. × *arnoldiana* (Rehder) Sarg. ex Rehder		Cultivated	*M. baccata* × *M. floribunda*				0	2	2×	
M. × *asiatica* Nakai		China, Korea	*M. sieversii* × *M. baccata*	Bot canker		Rootstock	4	16	2×, 4×	Zhi-Qin (1999), USDA (2014)
M. × *astracanica* hort. ex Dum. Cours.		Cultivated	*M. prunifolia* × *M. pumila*				0	1	2×	
M. × *atrosanguinea* (hort. ex Späth) C. K. Schneid.		Cultivated	*M. halliana* × *M. toringo*	Apple scab, Fire blight			0	2	2×	Le Roux et al. (2012)
M. × *dawsoniana* Rehder		Cultivated	*M. domestica* × *M. fusca*				0	2	2×	
M. × *domestica* Borkh.		Cultivated		Dessert, cider varieties			0	(1374)	2×, 3×	
M. × *hartwigii* Koehne		Cultivated	*M. baccata* × *M. halliana*	Apple scab			0	5	2×	
M. × *magdeburgensis* Hartwig		Cultivated	*M. pumila* × *M. spectabilis*				0	2	2×	
M. × *micromalus* Makino		Cultivated, China	*M. spectabilis* × *M. baccata*	Apple scab, Powdery mildew		Rootstock	9	16	2×	Fischer and Fischer (1999), Zhi-Qin (1999), USDA (2014)
M. × *moerlandsii* Door.		Cultivated	*M. purpurea* × *M. toringo*				0	2	2×	
M. × *platycarpa* Rehder		Cultivated	*M. domestica* × *M. coronaria*				0	7	3×, 4×	
M. × *purpurea* (A. Barbier) Rehder	Purple crab	Cultivated	*M. atrosanguinea* × *M. pumila*				0	5	2×	
M. × *robusta* (Carriere) Rehder	Siberian crab	Cultivated	*M. baccata* × *M. prunifolia*	Aphid, Apple scab, Fire blight, Powdery mildew		Rootstock	0	13	2×	Le Roux et al. (2012), Fischer and Fischer (1999), Hokanson et al. (2001), Marić et al. (2010), USDA (2014)

Table 1 continued

Malus species or hybrid	Common name	Origin	Hybrid parentage	Resistance to pests and diseases	Abiotic stress resistance	Physiology	NPGs seed accessions	NPGS unique field trees	Primary ploidy	References
M. × *scheideckeri* (L. H. Bailey) Späth ex Zabel		Cultivated	*M. floribunda* × *M. prunifolia*				0	2	2×	
M. × *soulardii* (L. H. Bailey) Britton	Soulard crab	Cultivated	*M. ioensis* × *M. pumila*				0	3	2×	
M. × *sublobata* (Dippel) Rehder		Cultivated	*M. prunifolia* × *M. toringo*	Fire blight		Rootstock	0	4	2×	Fischer and Fischer (1999), Hokanson et al. (2001), USDA (2014)
M. yunnanensis (Franch.) C. K. Schneid.	Yunnan crab	China, Myanmar, cultivated				Rootstock	0	16	2×	USDA (2014)
M. zhaojiaoensis N. G. Jiang		China					11	22	2×	
M. zumi (Matsum.) Rehder		Japan		Powdery mildew			0	3	2×	Fischer and Fischer (1999), Marı́c et al. (2010)
Malus hybrid							6	330		
Malus species							4	42		
Total							(1603)	(5004)		

Common name, origin, and hybrid parentages, according to GRIN Taxonomy (USDA 2014) are provided. Described species resistance to pathogens and abiotic stress, as well as desirable physiologies are given and referenced. NPGS inventory data for seed and PGRU orchards, as well as consensus ploidy information by species are listed were established as trees in home and community orchards. Seedling orchards continued to be planted as Americans moved westward, in part by John Chapman (1774–1845), also known as Johnny Appleseed. The millions of apple trees that resulted from planting seeds gave rise to a secondary center of diversity for *M.* × *domestica* in the United States. Recombination and segregation of alleles as a result of planting open-pollinated seeds resulted in millions of new genetic combinations. Particularly desirable seedling trees were then named and clonally propagated using traditional grafting methods. Many of the resulting cultivars have been maintained asexually for decades to centuries, such as 'Golden Delicious', 'Jonathan', McIntosh', and 'Hawkeye' (renamed to 'Delicious' and now commonly known as 'Red Delicious').

Apple breeding in the US

Breeding programs worldwide share similar goals, with differences largely based on regional or international consumer preferences and the specific biotic and abiotic challenges in the local areas of production. All breeders must balance key attributes, such as excellent and consistent fruit quality, with minimum levels of acceptability for a very large number of traits. US producers rated fruit flavor and crispness as key components of successful cultivars, while consumers particularly value crispness, size, color, and flavor (Yue et al. 2013). These traits are determined by numerous genetic factors and can be strongly affected by environmental influences (Kumar et al. 2012a, b; Longhi et al. 2012).

In the US, there are relatively few apple breeding programs (Online Resource 4). This deficit of breeding programs is a significant vulnerability for apple. In the future, it will be important to maintain a minimum number of breeders and breeding programs to support the large US apple industry. If the number of apple breeders and programs falls below a critical level, there will be a loss of advanced germplasm, a loss of critical institutional knowledge and resources, and too few new students receiving on-the-job training in this critical connection between apple genetic resources and commercial apple crop production.

Wild apple species, whether primary crop wild relatives or those that are more distantly related, offer many desirable traits that breeding programs could attempt to incorporate into commercial varieties (Table 1). Introgressing valuable alleles from apple crop wild relatives using traditional methods has been conducted successfully in several cases, yet it is challenging because alleles for undesirable attributes possessed by the wild relatives must be purged before a commercially viable cultivar can be released. Such purging takes several to many generations, which is a daunting prospect for any apple breeder. Because production attributes of the major progenitor species are typically closer to elite levels than those of other wild species and thereby presumably requiring fewer generations of purging of undesirable wild alleles, they have higher potential for more immediate use in breeding. US apple breeding programs have successfully used wild germplasm as parental materials. For example, the Purdue University, Rutgers, the State University of New Jersey, and the University of Illinois joint "PRI" program bred and released apple-scab resistant cultivars that contained a resistance allele from *Malus floribunda* Siebold ex Van Houtte after four or more generations of introgression (Janick 2002).

Access to performance records for wild or pre-bred germplasm is critical as methods for purging undesirable wild alleles become available. Allele-mining efforts may identify key individuals within wild species or segregating interspecific families that can be targeted for germplasm enhancement efforts. In addition, trait-predictive DNA tests and plants that reach reproductive maturity quickly will help future breeding efforts cycle through the generations and facilitate introgression (Kumar et al. 2012b).

Apple rootstock breeding programs are even fewer in number and more resource-intensive than scion breeding programs. Currently there is only one apple rootstock breeding program in the US. Objectives for this program include induction of dwarfing, early bearing, disease and insect resistance, and more recently, improved root architecture, absorption and translocation of nutrients, increased water use efficiency, and specific interactions with rhizosphere biota.

Available genomic tools

Access to the whole genome sequence of 'Golden Delicious' apple (Velasco et al. 2010), detailed genetic linkage maps, and marker systems (Jung et al. 2014) have enhanced the knowledge base available for apple genetic improvement (Dunemann and Schuster 2009;

Jung et al. 2014; Peace and Norelli 2009; Troggio et al. 2012). Trait-predictive DNA markers are beginning to be adopted in breeding programs for improved efficiency of seedling selections and parental mating designs (Kumar et al. 2010, 2012a, b; Evans 2013; Iezzoni et al. 2010; Marˇic et al. 2010). Several trait-predictive DNA tests have been developed and tested across different genetic backgrounds; yet many more are needed. "Fast" breeding approaches, such as the use of rapid cycling plants (Le Roux et al. 2012; Flachowsky et al. 2011), are useful for introgressing major-effect alleles for valuable attributes such as disease resistance into desirable backgrounds; however, alleles at multiple resistance loci must still be incorporated for durable resistance to pests and pathogens.

Functional loci also offer a way of characterizing diversity that may be more directly relevant to breeding programs. The analysis begins by identifying a set of loci through genome-wide association studies with phenotypic traits and extends it with locus specific re-sequencing of these loci within the diversity in the collection. Allele mining projects not only have direct impact on user access, but they are also important data to guide management decisions in the collection conservation process. These kinds of impacts all require a data infrastructure that is able to integrate the physical inventories of the collection to the digital data generated by genomic analysis.

"RosBREED: Enabling marker-assisted breeding in Rosaceae", a large multi-institutional grant, provided an opportunity for targeted efforts toward common breeding goals (Iezzoni et al. 2010). As a result, breeders of the three largest US apple scion breeding programs came to consensus on common phenotyping approaches and key materials for investigation (Evans et al. 2012; Schmitz et al. 2013). The inclusion of diverse breeding programs and the use of representative germplasm from multiple backgrounds have facilitated comprehensive genetic studies of valuable traits.

Urgency and extent of crop vulnerability and threats to food security

Genetic uniformity in cultivation and cultivar life spans

Although there are more than 7,500 named apple varieties, worldwide apple production is dominated by only 10–20 cultivars (Online Resource 5). In the US, 15 varieties accounted for 90 % of apple production in 2008, of which 'Red Delicious' alone was 24 % (U.S. Apple Association 2013). The relatively few cultivars that are produced on large acreages leads to near monocultures, and thus increases the crop vulnerability to diseases, pathogens, and environmental threats. Some of the key cultivars and breeding parents were first developed more than a century ago, such as 'Delicious' and 'Cox's Orange Pippin' (Noiton and Alspach 1996). Cultivars developed from 20th century breeding efforts have been planted intensively in the US in the last two decades, such as 'Gala' in 1965 from New Zealand, 'Fuji' introduced in 1962 from Japan, 'Cripps Pink' (Pink Lady^{TM}) in 1985 from Australia, and 'Honeycrisp' in 1991 from the University of Minnesota, US (Online Resource 5).

In the US, only three rootstocks represent 85 % of all trees planted in the past 20 years. These rootstocks are clones of 'Malling 9' (M.9) and related derivatives, 'Budagovsky 9' (B.9) and 'Malling 26' (M.26). Novel rootstocks that represent a wider genetic base and impart increased disease resistance and productivity in the orchard are increasingly being adopted by the US industry (Online Resource 6).

High density orchards can reach full production in 4 years, in contrast with the 8–10 years for traditional orchard production. Dwarfing rootstocks also increase productivity of apple trees by inducing early fruit bearing in grafted scions, reducing the time to flower by 2–7 years and by promoting fruit production instead of vegetative growth (Fazio et al. 2014). Trees can remain in production for 30 or more years, but may be replanted before that time to change cultivars. The desire to change cultivars may result from the presence of new diseases, pests, and changing climate combined with dynamic industry challenges and consumer demands. High density orchards have a shorter economic life span and are expected to be renewed on average every 12–16 years. The shorter orchard life spans will facilitate the incorporation of new desirable and disease-resistant cultivars into production systems.

Threats of genetic erosion *in situ*

Wild apple species are found either in large forests or scattered in woody patches in their native regions (Dzhangaliev 2003). Genetic diversity assessments of

M. sieversii suggest that the species has a panmictic diversity, likely due to the long life of some trees in the wild and the movement of seed and pollen over long distances (Richards et al. 2009b). The native habitats of most apple species are at risk of being lost due to grazing and other forms of human intervention (Food and Agriculture Organization of the United Nations 2012). Some regions, such as a particularly dry area in Kazakhstan, appear to have locally adapted allelic diversity that may be of particular interest (Hokanson et al. 1997; Forsline and Aldwinckle 2004).

Malus species are included on the global priority list for conservation of crop wild relatives (Khoury et al. 2013). Of 33 crop wild relatives assessed, more than 20 wild species were considered to be high priority for increased conservation efforts, and all the wild apple species still required further collection (Vincent et al. 2013). *Malus hupehensis* (Pamp.) Rehder, *M. sieversii*, and *M. crescimannoi* Raimondo are on the International Union for Conservation of Nature (IUCN) endangered, vulnerable, and near-threatened lists, respectively (IUCN 2013). *Malus* wild species are found in many forest habitats, and may be protected as part of parks, conservation areas, or national lands; however, *in situ* reserves specifically designated for conserving *Malus* species have not been established in the US.

Current and emerging biotic, abiotic, production, and accessibility threats and needs

The US apple crop is threatened each year by many pathogens, pests and abiotic stresses (Sutton et al. 2013). The continual threats of new pathogens and the adaptation of pathogens to control measures and pesticides jeopardize the industry. Resistant cultivars and rootstocks are the first defense against these threats, although many cultivars with consumer name-recognition do not possess desirable resistance traits. Rootstock breeding programs seek to provide the industry with materials that will provide some level of resistance to major rootstock pathogens. The use of traditional and/or integrated pest management and pathogen control in orchards is expensive and subject to environmental and legal regulations. In addition, new cultivars and rootstocks will need to be better adapted to the changing environment as global warming continues. Breeding programs rely on access to novel genetic resources and international quarantine programs play a key role ensuring that pathogen-free germplasm is imported into the US from other countries.

Diseases and pests

Both apple trees and fruit are susceptible to many pathogens and pests, in part because pathogens can be harbored in trees and orchard litter over many seasons. The pathogens present themselves differently depending upon whether they infect fruit or vegetative materials, and there are wide ranges in susceptibility across diverse *Malus* cultivars and species. The “Compendium of apple and pear diseases” lists many of the diseases and disorders of apple (Sutton et al. 2013). Other key resources include a review of apple biological and physiological disorders (Martins et al. 2013), fungal disease management (Holb 2009), and prediction of the spread of postharvest disease in stored fruit (Dutot et al. 2013). Pathogen threats are summarized in Table 2.

Diseases Apple scab (*V. inaequalis* (Cooke) G.Wint.) is the most economically important disease of apples in Northeastern North America; however, the disease can be effectively controlled with fungicides. The disease, its pathogen, and its control have been extensively researched and have been reviewed by MacHardy (1996). Sources of resistance to apple scab have been identified in many apple species (Table 1). Gene for gene interactions between *V. inaequalis* and *Malus* have been well characterized and eight races of the pathogen capable of overcoming various resistance genes have been documented (Bus et al. 2005).

Apple replant disease (ARD) causes stunting of young trees and substantial losses in production over the lifetime of the orchard (Sutton et al. 2013), and is of key importance because potent chemistries that were used to combat this problem (methyl bromide and chloropicrin) have disappeared and available virgin land optimal for orchard establishment has drastically decreased (Auvil et al. 2011). Common rootstocks M.9, B.9, and M.26 are very susceptible to the disease complex (Mac an tSaoir et al. 2011). When trees are planted in previous orchard locations, the presence of residual biological activity from the past orchard’s root systems affects the young roots, resulting in poor growth and productivity (Fazio et al. 2012, 2013). Several causative agents have been implicated in the etiology of ARD including *Cylindrocarpon destructans* (Zinssm.) Scholten, *Phytophthora cactorum* (Lebert et Cohn) Schröt., *Pythium* spp. Pringsheim, *Rhizoctonia solani* Kühn, and root lesion nematodes (Mazzola 1998). There are significant differences among rootstock varieties in their ability to grow in non-pasteurized ARD soils and the interaction between plants and the resident rhizosphere microflora (Isutsa and Merwin 2000; Gu and Mazzola 2003; Mazzola 2004; Mazzola and Manici 2012; Rumberger et al. 2007; St. Laurent et al. 2010; Yao et al. 2006). New rootstock cultivars derived from different species including *M.* × *robusta* (Carriere) Rehder, *M. prunifolia* and *M. sieversii* show tolerance to ARD.

Fire blight (*Erwinia amylovora* (Burrill) Winslow et al.) is a devastating disease of apple occurring throughout North America; however it is sporadic in its occurrence between years, locations and regions. Fire blight affects almost all plant parts, including rootstocks, by causing necrosis of woody tissues that can lead to plant death, particularly in young trees. The disease and its management have been reviewed (Vanneste et al. 2000; van der Zwet et al. 2012). It is a difficult disease to control and requires a combination of cultural practices, biological and chemical control for effective management. Resistance in the pathogen to streptomycin, the primary chemical control agent, exacerbates the difficulty of effective disease management in many regions of the US (McManus et al. 2002). Although fire blight is native to North America, high levels of resistance have been identified in several *Malus* species from Asia including *M. hupehensis, M. orientalis, M. prunifolia, M.* × *robusta* and *M. sieversii* (Table 1).

Powdery mildew (*Podosphaera leucotricha* (Ellis et Everh.) E.S. Salmon) occurs wherever apples are grown (Jones and Aldwinckle 1990). Its severity and resulting economic losses vary greatly between regions. The disease is particularly important in the Pacific Northwest of the US, where a netlike russeting can greatly reduce fruit value. Apple leaves, blossoms and fruit can be infected and fruit infections are common on severely infected trees. The disease is controlled by a combination of cultural practices and fungicide treatment. *M.* × *domestica* cultivars vary greatly in their susceptibility to powdery mildew and resistance is an important consideration in disease management. Sources of resistance have been identified in several *Malus* species including *M.* × *domestica, M.* × *robusta* and *M. sieversii* (Table 1).

Apple proliferation, caused by phytoplasmas [*Candidatus* Phytoplasma mali (Seemüller and Schneider 2004)], represents a major potential economic threat to US apple production and USDA-ARS-NPGS *Malus* collections. Apple proliferation has been documented in Europe. The causal agent of apple proliferation is graft-transmissible, and not seed-transmissible. The disease causes considerable economic losses (10–80 %) through the reduction of total yield, fruit size and vigor (Sutton et al. 2013). Control measures include removal of young infected trees, tree injection with tetracycline and control of insect vectors (leafhoppers). The causal agent can be detected by qPCR methods (Baric and Dalla-Via 2004; Wolfgang et al. 2013).

Blue mold (*Penicillium expansum* Link), is a fungal infection of punctures, bruises, or stems on fruit and is among the most important postharvest diseases of apple (Jones and Aldwinckle 1990). Financial losses from postharvest decay of apple can exceed 4.5 million dollars per year in the US (Rosenberger 1997). *P. expansum* is also of great concern to fruit processing industries due to its production of patulin, a highly toxic mycotoxin which can contaminate infected produce and its products. Sources of resistance to *P. expansum* have been identified in accessions of *M. sieversii* and *M. sylvestris* from the USDA-ARS germplasm collection (Jurick et al. 2011; Norelli 2013).

Alternaria blotch (*Alternaria mali* Roberts) is typically a foliar disease of warmer growing regions. It was first found in the US in North Carolina in 1988. The disease was later reported in the Southern US and was recently reported as a postharvest decay in Pennsylvania (Jurick et al. 2013). Alternaria blotch is usually not a major problem in Washington State or the northeastern US, although climate change may alter that situation and this disease is becoming increasingly important to production systems and breeding programs throughout the world. Additional information about the disease is available (Li et al. 2011, 2012b, 2013; Moriya et al. 2011; Saito and Taked 1984). Alternaria rot (*A. alternata* (Fr.) Keissl), is a common fruit rot in most apple growing areas; however, it seldom causes major commercial losses (Biggs and Miller 2005; Jones and Aldwinckle 1990).

Table 2 Pests and pathogens that threaten US apple production and product availability

Causal agent	Common name	Type	Symptom	Primary control
Erwinia amylovora (Burrill) Winslow et al.	Fire blight	Bacteria	Stem cankers, dead branches	Remove diseased leaf litter, benzimidazole fungicide, captan, copper
Candidatus Phytoplasma mali (Seemüller and Schneider 2004)	Apple proliferation	Phytoplasma		Disease-free trees in establishing new orchards, removal of infected young trees. Injection of oxytetracycline. IPM-based insecticide applications, cultural control, mating disruption
Alternaria mali Roberts	Alternaria blotch	Fungus	Brown leaf spots in late spring, turn to ash gray	Copper spray, antibiotics, remove source of infection
Alternaria alternata (Fr.) Keissl	Alternaria rot	Fungus	Round, brown to black, dry, firm, shallow lesions on fruit around skin breaks or at the calyx or stem depression	Disinfect wooden picking bins. careful handling of fruit to prevent wounds. rapid postharvest removal of field heat from fruit. chlorine in dump tank
Botryosphaeria dothidea (Moug.) Ces. et De Not	White rot	Fungus	Reddish-brown spots around lenticels, may have red halos, dark brown skin color, mushy flesh	Remove inoculum sources, foliar fungicides during leaf growth, sulfur, strol-inhibitors, strobilurins
Botryosphaeria obtusa (Schwein.) Shoemaker	Black rot (fruit)/frog eye leaf spot	Fungus	Brown and black spots on fruit, decayed tissue is firm, small, purple specks on leaves	Tree removal, resistant rootstock
Glomerella cingulata (Stoneman) Spauld. et H. Schrenk anomorph: *Colletotrichum gloeosporioides* (Penz.) Penz. et Sacc., *C. acutatum* J. H. Simmonds	Bitter rot	Fungus	Brown spots on fruit, ooze gelatinous salmon-pink mass of spores	Remove decayed fruit from orchard, thiabendazole drench, fludioxonil and pyrimethanil drench, pseudomonas syringae biocontrol
Gymnosporangium clavipes Cooke et Peck	Quince rust	Fungus	Fruit calyx deformation, orange spores in tube-like structures	Maintain low levels of orchard mites, strobilurin fungicides
Gymnosporangium globosum (Farl.) Farl.	American hawthorn rust	Fungus	Galls on twigs	Remove prunings and mummified apples, fungicide spray for fruit rot
Gymnosporangium juniperi-virginianae Schwein.	Cedar apple rust	Fungus	Yellow spots that turn orange or red on leaves, tube like structures on underside of leaves, galls	Fungicides, removal of nearby junipers
Peltaster fructicola Johnson, Sutton et Hodges, *Geastrumia polystigmatus* Batista et M.A. Farr, *Leptodontium elatus* (F. Mangenot) de Hoog*, Gloeodes pomigena* (Schwein.) Colby	Sooty blotch and fly speck complex	Fungus	Sooty smudges or solive-green spots on mature fruit,clusters of black shiny specks on fruit	Fungicides, removal of reservoir hosts
Penicillium expansum link *Penicillium* spp.	Blue mold	Fungus	Tan to dark brown decayed fruit tissue	
Phyllosticta solitaria Ellis et Everh.	Fruit blotch	Fungus	Light gray or dark leaf spots, spots to blotches on fruit	

Table 2 continued

Causal agent	Common name	Type	Symptom	Primary control
Podosphaera leucotricha (Ellis et Everh.) E.S. Salmon	Powdery mildew	Fungus	Defoliation, stunted growth, silver-gray appearance	Remove diseased materials, fungicide
Valsa mali	Valsa canker	Fungus		Removed diseased tissue, fungicide
Venturia inaequalis (Cooke) G. Wint.	Apple scab	Fungus	Black or brown lesions on leaves, buds or fruits	Fungicide sprays, removal of mummified fruit
Various	Apple replant	Fungus, Nematodes	Witches' broom branches, leaf rosettes	Fungicide sprays
Popillia japonica Newman	Japanese beetle	Insect	Skeletonized feeding on foliage and chewing damage on fruit	
Choristoneura rosaceana Harris	oblique-banded leafroller	Insect	Early-season fruit drop, scarred fruit remaining on tree	IPM-based insecticide applications, cultural control, mating disruption
Conotrachelus nenuphar Herbst	Plum curculio	Insect	Eggs laid in fruit resulting in scars or bumps on fruit skin and larval feeding internally	Insecticide
Cydia pomonella Linnaeus	Codling moth	Insect	Larvae penetrate fruit and feed internally	Biological control, dormant season treatments
Diaspidiotus perniciosus Comstock	San Jose scale	Insect	Reduced tree vigor, reddish purple ring surrounding feeding sites on fruit	Scouting, monitoring, dormant oil
Dysaphis plantaginea Passerini	Rosy apple aphid	Insect	Curled, crimson leaves; bunched, stunted, malformed fruit	Scouting, monitoring, insecticide
Eriosoma lanigerum Hausmann	Woolly apple aphid	Insect	Cottony-white aerial colonies, honey dew and sooty mold on fruit, galls on plant parts	Parasitic wasps for IPM, pruning, chemical control
Grapholita molesta Busck	Oriental fruit moth	Insect	Flagging on young shoots, larvae penetrate fruit and feed internally	Insecticide
Halyomorpha halys Stål	Brown marmorated stink bug	Insect	Indented, discolored depressions on fruit surface with corky flesh beneath	Insecticide
Orthosia hibisci Guenée	Green fruitworm	Insect	Dropped fruit, larve feeding cavities and scarring	Insecticide
Rhagoletis pomonella Walsh	Apple maggot	Insect	Eggs laid in fruit resulting in internal larval feeding and damage	Biological control, insecticides
Typhlocyba pomaria McAtee	White apple leafhopper	Insect	Mottling on leaves, honeydue on leaves and fruit	Insecticide
Panonychus ulmi Koch	European red mite	Mite	Leaf bronzing	Insecticide, behavioral control

Insect pests Persistent pests of apple can cause serious economic damage if they are not managed appropriately. These pests belong to classes found within the phylum Arthropoda, Insecta (insects) and Arachnida (mites) and can be divided into two categories, direct and indirect pests. Direct pests attack fruit and fruiting buds, causing visible, immediate injury. Although some damage may be cosmetic, it does not affect nutritional value or flavor, it reduces the aesthetic quality of the fruit. Indirect pests attack foliage, roots, limbs or other woody tissues leading to problems such as reduced tree vigor, fruit size and/or quality and susceptibility to opportunistic secondary infections. Each growing region is prone to injury from a unique complex of pests. The pest species and groups described here are those considered to be of greatest concern.

Codling moth (*Cydia pomonella* Linnaeus) and Oriental fruit moth, *Grapholita molesta* (Busck), are serious worldwide pests of pome (apple and pear) and stone fruit, respectively. Both are internal feeders at the larval stage, destroying developing fruit. Codling moths can damage 80 % of an apple crop without intervention. Monitoring methods include pheromone traps in combination with degree-day egg hatch models for detection and timing insecticide applications. In addition, mating disruption has also proven promising (Agnello et al. 2006; Howitt 1993).

Plant pests (Family Miridae), especially *Lygus* species, and stink bugs (Family Pentatomidae) are pests of apple throughout the world. Although adults and nymphs feed on herbaceous and/or woody plants, they also will feed regularly on deciduous tree fruit and shoots. In apple, early season pre-bloom feeding can result in bud abscission while feeding after fruit set results in slight dimpling to deeply sunken, distorted areas with corky flesh beneath. White sticky rectangular traps hung from trees have been used to monitor tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois). More recently, brown marmorated stink bug (BMSB) *Halyomorpha halys* Stål has become a devastating pest of apple in the US (Leskey et al. 2012). BMSB has an extremely wide host range in both its native home and invaded countries. It feeds on numerous tree fruits, vegetables, field crops, ornamental plants, and native vegetation. In 2010, population explosion caused severe crop losses to apples, peaches, vegetables and row crops in the mid-Atlantic region of the US Intervention in apple orchards relies on broad spectrum-insecticides, especially pyrethroids. This practice disrupts IPM programs leading to secondary pest problems that usually are controlled by natural enemies (Leskey et al. 2012).

The indirect pest, European red mite (ERM), *Panonychus ulmi* (Koch), and two-spotted spider mite (TSM), *Tetranychus urticae* Koch, are worldwide pests of apple with up to ten generations of ERM and nine generations of TSM possible in a growing season. Foliar feeding results in bronzing of leaves with moderate to severe infestations reducing yield by decreasing fruit size and promoting premature drop. Damaging populations also can affect fruit buds the following year. Monitoring involves scouting for eggs on twigs and spurs in the dormant season and foliar examinations throughout the growing season to establish infestation levels. One or more pre-bloom oil applications along with miticide treatments have been used for control throughout the growing season. Natural enemies such as predaceous mite species and ladybird beetles can reduce populations if chemicals that are harmful to these beneficials are avoided (Agnello et al. 2006; Howitt 1993).

Rosy apple aphid, *Dysaphis plantaginea* (Passerini), is found in most apple growing regions worldwide. Oval-shaped eggs are laid on twigs and branches in the fall and hatch into nymphs in the spring from the silver tip to one half inch green stage of bud development. Nymphs feed on leaves and fruit buds until leaves begin to unfold and inject a toxin as they suck sap that results in leaf curling, and potential abscission and deformed and stunted fruit. Honeydew produced by colonies can lead to growth of sooty mold. Predators such as ladybird beetles, syrphid flies, lacewings and predatory midges as well as parasitic wasps are capable of providing effective biological control if chemicals toxic to these beneficial insects are avoided (Agnello et al. 2006; Howitt 1993).

Abiotic stress Climate change will affect future apple crop production in the US and worldwide. Changes in weather patterns that result in warmer winters, earlier springs with unpredictable spring frosts, and altered rainfall patterns and availability will affect where and what types of apple crops can be grown (Dempewolf et al. 2014; Jenni et al. 2013). A focus on breeding for late bloom to avoid spring frosts, and adaptation to fluctuating temperatures will be important. In South Africa, there was an average of a

1.6 day increase per decade in the time of full bloom date of apple over the past 37 years (Grab and Craparo 2011).

Atkinson et al. (2013) examined the impacts of declining winter chill on the production of temperate perennial crops in the northern hemisphere. Models predict that declining winter chill will affect dormancy induction, satisfaction of specific dormancy requirements, and the timing of bud break, and these in turn will limit fruit production. The current lack of understanding of these features in apple cultivars is a concern. There will be a future need for low-chill cultivars, coupled with changes in crop management practices to better tolerate low chill conditions (Atkinson et al. 2013; Luedeling et al. 2011). A strong genetic component underlying the timing of both reproductive and vegetative bud break in apple was reported by Labuschagné et al. (2002a, b). Identification of genetic markers for "depth of dormancy" may aid in breeding programs focused on these issues (Campoy et al. 2011). Celton et al. (2011) identified genes involved in cell-cycle control that were linked to QTLs for chilling and heat requirement in apple. Furthermore, the importance and identification of major QTLs for initial vegetative bud break were reported by Van Dyk et al. (2010), Labuschagné et al. (2003) and Mehlenbacher and Voordeckers (1991). Recently, Gottschalk and van Nocker (2013) published important information on diversity in seasonal bloom time and floral development among apple species and hybrids in the US. This information will aid researchers breeding for climatic adaptation in bloom time. Genomic research on flowering in trees also holds promise for improvements in this area (Hanke et al. 2012).

Changing climate conditions may also affect water availability during the growing season, causing some regions to experience drought, and other regions, with poorly drained soils, to be waterlogged (Bassett et al. 2011). Drought stress causes wilting, leaf yellowing, advanced leaf fall and premature fruit ripening or fruit drop. Sunburn may also cause leaf and fruit scorching. Young trees are more sensitive to these stresses. In contrast, waterlogged trees can easily become infected by Phytophthora root and crown rot, which leads to premature fruit ripening, a decrease in quality, and overall orchard decline. Identification of drought or water logging resistant rootstocks may be the most promising solution to this potential threat.

A bright spot in the consequences of climate change was highlighted by Bartomeus et al. (2013) in their study on climate change and pollinators. They combined 46 years of data on apple flowering phenology with records of bee pollinators over the same period. When key apple pollinators were considered, they found extensive synchrony between bee activity and peak apple bloom. This synchrony was attributed to complementarity among bee species' activity periods, and also a stable trend over time due to differential responses to warming climate among bee species. The simulation model confirmed that high biodiversity levels might ensure synchrony among plant phenology and pollinators and therefore ensure pollination function.

Accessibility Most *Malus* species considered to be wild crop relatives of potential interest in breeding are not native to the US. Access to these novel plant genetic resources depends on legal and phytosanitary requirements in the US and abroad. International regulations affect movement of germplasm between countries, and some governments are sensitive to the international access to materials in the NPGS. International treaties may also limit or control the extent of access to genetic resources. The International Treaty on Plant Genetic Resources for Food and Agriculture governs movement of plant genetic resources among signatory countries. At this time (2014), the US has not signed the treaty. *Malus* is listed as an Annex I crop, and thus its movement between countries is covered under the treaty (Food and Agriculture Organization of the United Nations 2009). Material transfer agreements, patents, or restrictive agreements may impede acquisition and distribution of valuable germplasm. Politics or conflicts within a source country may make expeditions to remote areas or germplasm exchanges impossible. Expeditions to source countries may also be limited by budgets. Access of the US to *Malus* genetic resources varies on a country-by-country basis, and in some cases, significantly limits the ability to collect and conserve the majority of *Malus* species, including the primary crop wild relatives, that are not native to the US.

Upon arrival in the US, clonal apple germplasm must be inspected and then tested for pathogens in quarantine before release to importers. A total of 50 slots are available for apple clonal imports annually. In contrast, apple seeds can be brought into the US with phytosanitary permits, but without quarantine requirements. The presence of an insect pest that cannot be eliminated by fumigation necessitates destruction of the imported plant material. Infected clones are subjected to therapy to remove detected pathogens. The efficiency of the quarantine process, as well as the ability to keep imported introductions alive during quarantine, is directly affected by the funds and resources committed to this activity.

Status of plant genetic resources in the National Plant Germplasm System available for reducing genetic vulnerabilities

Germplasm collections and *in situ* reserves

The USDA-ARS-NPGS apple collection is maintained by the Plant Genetic Resources Unit (PGRU) in Geneva, NY. The field collection of apple cultivars and *Malus* species is located approximately 2 miles from the physical location of the PGRU, on the campus of Cornell University's New York Agricultural Experiment Station. The PGRU has greenhouse facilities on-location as well as laboratory and −20 °C storage facilities. The apple collection was initiated in 1984 as a clonal repository in the NPGS (Barton 1975; Brooks and Barton 1977). Many of the cultivars in the *Malus* collection were provided by US breeders (particularly at Cornell University) (Way 1976; Way et al. 1990). Many of the species represented in the collection were obtained through plant exploration trips.

Holdings

The USDA-ARS Plant Genetic Resources Unit maintains a total of 5004 Malus field accessions and 1603 seedlots in Geneva, NY. Of these, 2,800 trees are grafted, and 2,204 have been grown from seeds collected from the wild. In addition, 1,489 trees in seven F_1 pseudo-testcross populations from 'Gala' crossed with selected *M. sieversii* seedlings are being used in many different genetic studies.

The permanent field collections are maintained as clones and are planted on the semi-dwarf rootstock 'EMLA 7' at 12 ft × 20 ft spacings. Trees are grafted in the nursery blocks and then planted in duplicate in the fields. The second tree is removed once the primary tree is established, thus leaving one grafted tree per accession, for a total 3,070 trees in the main orchards. All trees are labeled with the row and tree number, Plant Introduction number (PI), local inventory tracking number (GMAL), variety name, and genus and species.

The 258 trees in the core collection were selected in the 1990s based on species representation and diversity. The diversity of these trees, in relation to materials in the collection was described by Gross et al. (2013). The 258 core collection trees are on 'Budagovsky 9' rootstocks and were planted at a 7 × 20 ft spacing, with one tree per accession. All the core trees are also present in the permanent collection, so in effect, the materials in the core collection are present in duplicate.

Two wild species orchards of seedling trees were derived from seeds collected on plant exploration trips. They are planted as half-sib families, with multiple seedlings originating from the same maternal tree. The orchards were planted with 5 ft between trees, 6 ft within the double rows, and 20 ft between two double rows. One seedling orchard contains *M. sieversii* seedlings from seeds collected from four trips to Central Asia between 1989 and 1996. The second seedling orchard has trees representing many other wild *Malus* species from throughout the world (Table 1). Accessions of *M. doumeri* (Bois) A. Chev. are maintained in the greenhouse, due to its chilling sensitivity.

Most of the seed accessions (more than 170,000 seeds) from original collection trips and are stored in heat–sealed aluminum layered bags at −20 °C. An additional collection of 63,000 seeds, termed the "Botany of Desire" seeds, collected from open-pollinated fruits of the *M. sieversii* trees in the *Malus* collection, are available for distribution. This seed lot was developed for distribution in response to the demand for seeds spurred by the popularity of the book "Botany of Desire", by Pollan (2001).

A total of 548 seed accessions originally collected from wild species have been backed up at the USDA National Center for Genetic Resources Preservation (NCGRP) in Fort Collins, CO, US. In addition, 2,335 clones have been cryopreserved as dormant buds and are maintained in liquid nitrogen vapor conditions at NCGRP (Forsline et al. 1998). A portion of these will be reprocessed due to low viabilities. For cryopreservation, a total of 120–140 buds are processed per clonal accession. Accessions that have at least 40 % viability and 60 predicted living buds are considered to be stored in the NCGRP base collection. Ten sub-lots of 10 buds for each accession are stored at NCGRP. Within a year of placement in storage, two sub-lots of 10 buds each are sent back to PGRU to test the baseline recovery level. The goal is to cryogenically back-up >95 % of the permanent *Malus* accessions. At the current time, approximately 30 *Malus* accessions are processed for cryopreservation each winter. Materials are periodically monitored so that accessions can be reprocessed for cryostorage if necessary. If a tree is lost in the field due to disease or other factors, it can be rescued from the NCGRP cryogenically stored buds.

Genetic coverage and gaps

Cultivated *Malus* are represented by dessert, cider, and ornamental types and key cultivars of breeding and historical significance are in the NPGS *Malus* collection. The collection overlaps with international gene bank and arboreta collections of crabapples. Fingerprinting efforts are underway to determine the genetic overlaps among these diverse collections. These data will be used to ascertain if highly diverse or unusual materials should be added to the NPGS collection. Standard reference cultivars, such as differential hosts, for evaluating disease resistance will be added to the collection.

Plant exploration trips focused on wild species have made the USDA collection one of the most representative *Malus* species collections in the world; however, there are still many gaps. Collection trips for *M. sieversii* in Central Asia and *M. orientalis* from the Caucasus region were particularly successful. Diversity assessments suggest that accessions from these regions represent the widespread diversity within the two species, although some unique habitats and extended collection ranges may offer novel variation (Volk et al. 2008a). The diversity of *M. sieversii* in western China (a region in which the NPGS has no *M. sieversii* representation) should be compared to that already obtained from Kazakhstan and other Central Asian countries. The NPGS has 62 accessions of *M. sylvestris*, a species native to Europe, that are maintained clonally. Seeds collected from wild populations in Georgia, Albania, and the former Yugoslavia are available and will be germinated to augment the representation of this species in the NPGS field collection. Additional populations representing native, non-hybridized stands of *M. sylvestris* should be added to the collection.

Chloroplast data analyses have identified several *Malus* species as particularly distinctive genetically including *M. doumeri* and *M. florentina* (Zuccagni) C. K. Schneid. These are represented by 1 and 3 trees, respectively, in the NPGS, and these collections should be augmented (Volk et al. submitted). In addition, there are numerous described species for which there is no representation in the NPGS. Without access to materials, novelty or relationships with existing wild species in the NPGS cannot be determined. These species include: *Malus baoshanensis* G. T. Deng, *Malus chitralensis* Vassilcz., *M. crescimannoi, Malus jinxianensis* J. Q. Deng et J. Y Hong, *Malus leiocalyca* S. Z. Huang, *M. maerkangensis* M. H. Cheng et al., *Malus muliensis* T. C. Ku, and *Malus spontanea* (Makino) Makino. The 18 species with individuals that originated from China vary in their adequacy of representation in the NPGS. There are four species in the NPGS native to North America: *M. fusca, M. ioensis, M. coronaria*, and *M. angustifolia* (Khoury et al. 2013). Fingerprinting data suggest that most of the diversity of *M. fusca* has been captured in the collection, as determined by a comparison between NPGS materials and those in herbaria (Routson et al. 2012). Ecogeographical and genetic diversity analyses are needed for the three *Malus* species native to central and eastern North America to determine the adequacy of their representation in the NPGS. Similar analyses should be performed for all wild *Malus* species.

Acquisitions

Following the establishment of the PGRU, explorations were initiated in 1987 with the collection of four North American wild *Malus* species (Dickson et al. 1991; Dickson 1995). From 1989 to 1996, four expeditions were made to Central Asia to collect *M. sieversii* (Luby et al. 2001; Forsline et al. 2003). Three more expeditions to China, Russia and Turkey collected nine other *Malus* species (Aldwinckle et al. 2002). Many more apple varieties and wild *Malus* species were obtained from exchanges with arboreta and gene banks worldwide (Online Resource 7).

Collection size and priority is at the discretion of the curator, with guidance provided by the Apple Crop Germplasm Committee (CGC). Due to the limited budget and field space, the acquisition of new materials must be prioritized and it is a decision that is based on existing genetic gaps, potential risk of genetic erosion of the material, novelty, desirability and need in the user community, quality passport data, and the freedom to distribute. Materials are not acquired that have intellectual property rights or that are regulated transgenics.

Maintenance

To assure that healthy *Malus* germplasm is available for stakeholders, living collections are maintained using well-established horticultural and pest management methods. Apple fire blight is a significant challenge. To reduce fire blight incidence, most of the permanent apple plantings are grown on 'EMLA 7', a semi-dwarf rootstock that limits the vigorous growth that enhances "shoot blight". Additionally, prohexadione calcium ("Apogee", a growth retardant that reduces shoot growth) is applied annually to all apple plantings to minimize fire blight (Forsline and Aldwinckle 2002). An online Network for Environment and Weather Applications (NEWA) fire blight disease forecasting model that is based on weather data is used to predict the potential of fire blight outbreaks and determine the proper timing of pesticide application for disease control (Cornell University 2013). The trees are pruned every winter, and also pruned late in the season to remove fire-blight infected shoots.

Regeneration

The PGRU *Malus* collection is maintained as trees and seeds. The *Malus* seed collection is mostly comprised of original wild-collected seeds that are intended for routine distribution. Subsets of some of these seed lots have been planted. In 2005–2006, controlled pollinations were performed among individuals in *M. sieversii* core set trees to capture the diversity represented by two collection sites in Kazakhstan (Volk et al. 2005). One *M. sieversii* orchard may be removed in 2015, after selected trees are transferred to the grafted orchard, to make room for new acquisitions.

Distributions and outreach

Germplasm is distributed as seeds, dormant bud wood, summer bud wood, leaves, flowers, pollen, fruit, and DNA, and requests are received from the Genetic Resources Information Network (GRIN; USDA 2014). A total of 87,991 *Malus* samples were distributed between 1983 and 2012 (Table 3). A New York state inspector is consulted for all international shipments.

Most plant material is distributed as dormant cuttings in mid-winter. Summer budsticks are also distributed, which are amenable to green tissue propagation. Pollen, seed, leaf, or fruit samples are provided as requested if they are available and permitted by regulations of the receiving country or state. Occasionally flowers will be bagged for self-pollination or cross-pollinated at the request of researchers who require seeds of known parentage. There are an increased number of requests for DNA samples, which are easier to ship overseas than living plant material. PGRU has established DNA stocks for some selected accessions for distribution.

Many college classes, stakeholder groups, growers, and researchers from the US and internationally visit the *Malus* collection. Open houses are held during the fall harvest season to demonstrate the diversity of the collection.

Associated information

Data access

All passport and phenotypic data are stored in GRIN (USDA 2014). The GRIN database is transitioning to an updated version, GRIN-Global. Gene, sequence, marker, diversity, trait, and trait locus data for *Malus* is available through the Genome Database for Rosaceae (GDR; www.rosaceae.org; Jung et al. 2014). GDR is a curated and integrated web-based relational database that provides centralized access to Rosaceae genomics, genetics, and breeding data and analysis tools to facilitate breeding and research. Other key websites relating to the apple industry and genetic resources are listed in Online Resource 8.

Passport information

Passport data are recorded in GRIN and are publicly available (USDA 2014). Passport data usually include: collection site, general description of the site and the accessions, latitude, longitude, GPS coordinates, elevation, and habitat information. Other information recorded in GRIN include accession number (PI and/or GMAL), collector (if from an exploration), date when accession was received, backup status, accession name, availability, narrative (about the accession), source history (development or collection information), pedigree, observation (phenotypic and genotypic data), and vouchers of the accessions (digital images).

Genotypic characterization data

Most of the diploid accessions in the *Malus* collection have been genotyped using microsatellite markers. Datasets for seven SSRs were used to assess genetic diversity and determine species-specific core collections for 949 *M. sieversii* and 776 *M. orientalis* accessions collected from the wild and grown in two PGRU orchards (Volk et al. 2005, 2008a, 2009a, b; Richards et al. 2009a, b). A dataset of seven SSR was used to assess the genetic variation and distribution of *M. fusca* (Routson et al. 2012). Analyses of the profiles of nine SSRs (across 2114 accessions) identified "duplicates" in the clonal collection as well as coverage of the primary core collection (Gross et al. 2012, 2013). These microsatellite datasets were also used to identify interspecific hybrids among progenitor apple species (Gross et al. 2011). Four regions of the chloroplast have been sequenced from 412 accessions to describe genetic differences among 30 *Malus* species (Volk et al. submitted).

Phenotypic evaluation data

The NPGS apple collection has been characterized for traits of botanical, horticultural, and breeding interest. Botanical traits that aid in accession identification include anther color, calyx traits and color, carpel number and arrangement, flower traits and colors, leaf traits, and seed and shoot traits. Phenotypic traits relating to production and breeding include chemical (soluble solids), cytological (ploidy), disease (blossom and shoot fire blight), growth (tree vigor), morphology (fruit traits and colors), and phenology (bud break, bloom time, harvest season, and production description). About 2,500 accessions in the collection have been phenotyped using a 28-trait descriptor set (Online Resource 9).

Plant genetic resource research associated with the NPGS

Goals and emphases

To help breeders and others make informed use of the apple germplasm, PGRU actively pursues various germplasm research projects to develop genetic knowledge about the collection and traits important to apple variety improvement. These goals are accomplished mainly through collaborations by providing research support. When resources permit, in-house research projects are conducted. Currently, PGRU in-house research focuses on characterizing fruit quality and phenology traits of *Malus* in the permanent collection, and using next-generation SNP markers to evaluate the diversity in the collection (Gardner et al. 2013). Efforts are underway to continue to image fruits and evaluate trait performance in wild *Malus* accessions.

Significant accomplishments

The NPGS *Malus* collection is one of the most genetically diverse collections in the world. Collaborations with scientists from across the world have resulted in many accomplishments. Cryopreservation research demonstrated that storage of dormant budwood of *Malus* in liquid nitrogen is reliable and can be used for backing up a germplasm collection (Forsline et al. 1998; Seufferheld et al.

Table 3 Distribution of apple materials from PGRU between 2008 and 2013

Year	No. plants distributed
2008	7,046
2009	3,653
2010	4,082
2011	5,448
2012	6,311
2013	6,627

1999; Jenderek et al. 2011; Volk et al. 2008b; Walters et al. 2011). Multiple explorations in Central Asia have secured and preserved valuable wild *Malus* germplasm, especially for *M. sieversii* (Luby et al. 2001; Forsline et al. 2003). Evaluations of the wild *Malus* germplasm in the last 20 years has uncovered new resistance sources against fire blight (Momol et al. 1999; Aldwinckle et al. 1999; Luby et al. 2002; Forsline and Aldwinckle 2004; Volk et al. 2008a; Fazio et al. 2009; Norelli et al. 2009, 2011), apple scab (Luby et al. 2006; Volk et al. 2008a), cedar apple rust (*Gymnosporangium juniperi-virginianae* Schwein.) (Biggs et al. 2009; Volk et al. 2008a; Fazio et al. 2009), blue mold (Janisiewicz et al. 2008; Jurick et al. 2011*)*, bitter rot (*Colletotrichum acutatum* J. H. Simmonds) (Biggs and Miller 2001; Kou et al. 2013; Jurick et al. 2011), superficial scald (a physiological disorder), *Phytophthora*, *Rhizoctonia*, apple maggot (*Rhagoletis pomonella* Walsh) and plum curculio (*Conotrachelus nenuphar* Herbst) (Myers et al. 2008). *Malus* collections in Geneva also have been used to study cold hardness (Luby et al. 1999), red pigmentation (cyaniding-3-*O*-galactoside) concentration in flesh and antioxidant capacity (Rupasinghe et al. 2010), anthocyanin content, *MYB*10 R_6 allele (Van Nocker et al. 2011), dormant bud break control and phenology (Gottschalk and van Nocker 2013), fruit abscission related traits (Sun et al. 2009), water use efficiency and drought stress tolerance (Bassett et al. 2011), characterization of the *Ma* (*malic acid*) locus that controls pH and titratable acidity of apples (Xu et al. 2011), and apple fruit shelf life (ripening-specific *MdACS3* gene) (Wang et al. 2009). Studies of *Malus* diversity (Benson et al. 2001; Hokanson et al. 1998, 2001; Lamboy et al. 1996; Richards et al. 2009a, b; Volk et al. 2008a, 2009a, b), construction of core collections (Lamboy et al. 1996; Forsline 1996; Hokanson et al. 1998, 2001), and identification of interspecific hybrids between *M. domestica* and wild *Malus* species (Gross et al. 2011) were performed using microsatellite markers. Wide distribution of the *Malus* germplasm and associated information to researchers and stakeholders in the US has significantly enhanced the scientific knowledge about apple and the *Malus* genus as a whole and has helped accelerate the use of *Malus* germplasm for the development of new apple varieties.

Other genetic resource capacities

In the FAO database, 167 *Malus* collections are present in 58 countries (Online Resource 10). Countries with the largest genebank collections of *M.* × *domestica* include Switzerland (6617), Italy (4403), Russian Federation (3586), Austria (2731), France (2648), United Kingdom (2167), Brazil (1812), Kazakhstan (1719), USA. (1548), and Japan (1509) (Online Resource 10, Fig. 1). The US (5051), Italy (710), and Japan (678) have the largest collections of accessions of wild *Malus* species (Online Resource 10). The European Cooperative Programme for Plant Genetic Resources EURISCO database lists Switzerland (8878), Ukraine (2665), United Kingdom (2256), and Austria (2168) as the largest "European" apple collections (Online Resource 11; European Cooperative Programme for Plant Genetic Resources 2013).

The Global Biodiversity Information Facility (GBIF) database was queried to identify the georeference information for *Malus* accessions of wild origin in that database. GBIF data contributors include herbaria, genebanks, and other collections (not necessarily all "living" collections). Figure 2 illustrates the distribution of wild *Malus* materials in the GBIF database, and is overlaid with the georeference information for the NPGS *Malus* wild species collection (without reference to specific species). The map demonstrates that wild *Malus* genetic resources are much more widely distributed than what is currently available through the NPGS. The USDA likely has the most diverse collection of *Malus* species maintained *ex situ* in the world. Species representation is still inadequate and access to many species is difficult in the current political environment. Wild species are vulnerable, and at this time, conservation of many wild species must happen within their countries of origin.

The NPGS does not have dedicated *in situ* reserves for North American wild *Malus* species. Native North American wild apple species are present within federal, state, county, and municipal lands, as well as on Tribal Lands and private lands. A number of apple collections are maintained at universities, in arboreta, in botanic gardens, and privately in the US (Online Resource 8).

Publicly available "genomic stocks" of apple are not maintained; however, the PGRU does maintain seven 'Gala' × *M. sieversii* (GMAL 4335, GMAL 4448, GMAL 4455, GMAL 4331, GMAL 4334,

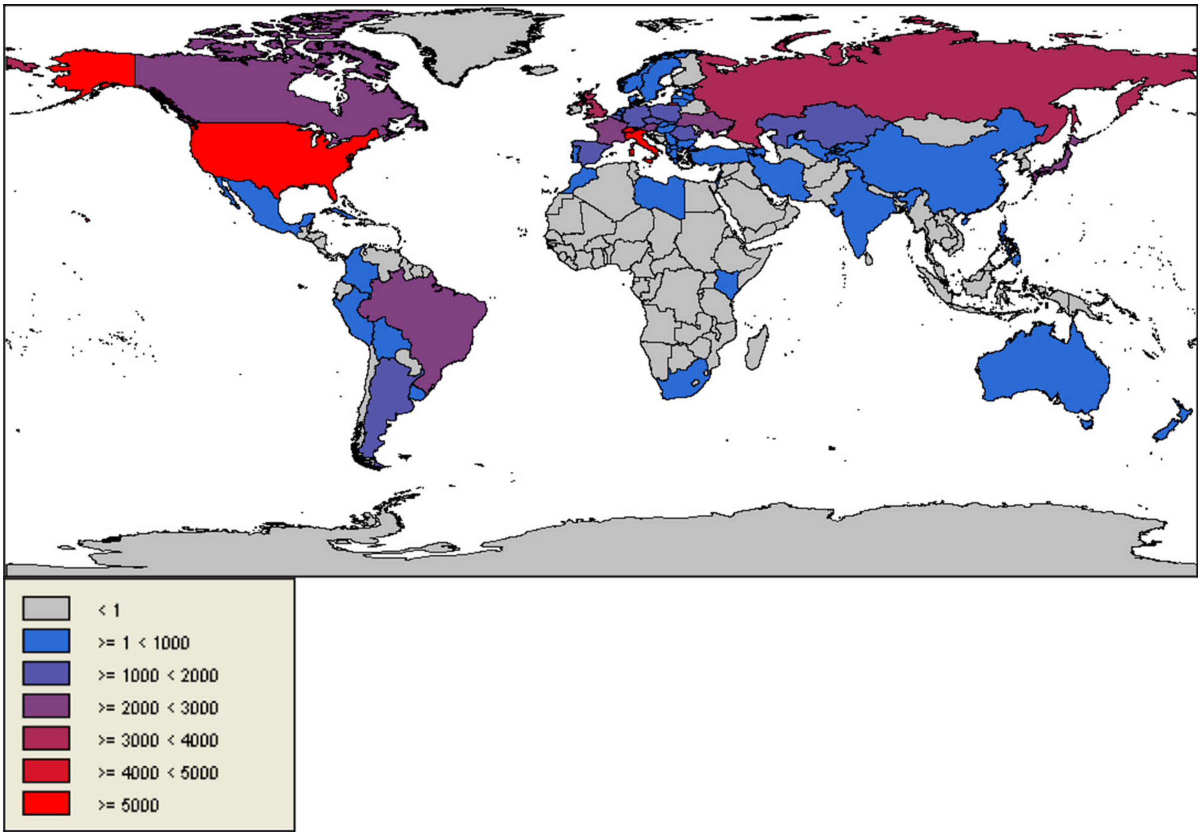

Fig. 1 Countries listed with *Malus* collections in the FAO database in 2013. Colors reflect the number of accessions within collections for each country. (Color figure online)

GMAL 4333, and GMAL 4327) F_1 populations of seedling trees that are available for research.

The Apple CGC, as an advisory committee, is a group of scientists and industry representatives that provides analyses, data, and recommendations on apple genetic resources. The Apple CGC plays a role in identifying gaps in US collections, assisting the curator in identifying duplication, prioritizing traits for evaluation, assisting in regeneration projects, and identifying germplasm at risk of being lost. US *Malus* genomics, genetics, and breeding communications are coordinated in part by the US RosEXEC. This group comprises Rosaceae scientists and industry representatives (along with some international community representatives) and serves to unify efforts across the diverse Rosaceae crops. At the international level, Rosaceae genomics, genetics, and breeding scientists are served by the Rosaceae International Genomics Initiative (RosIGI).

Apple grower and consumer organizations are present at the national and statewide levels. These groups support growers by holding meetings on marketing, crop outlooks, statistics and government affairs. They also provide cultivar, nutrition, and use information for consumers (Online Resource 8).

Prospects and future developments

The US apple crop is vulnerable because of the low number of cultivars that are in production, the longevity of orchards, and the limited number of US breeding programs. Increased production expenses, pathogens and pests, and high consumer expectations are driving the need for a range of improved cultivars that offer improved resistance to biotic and abiotic stresses as well as year-round high product quality for consumers. Traditional breeding programs are facing

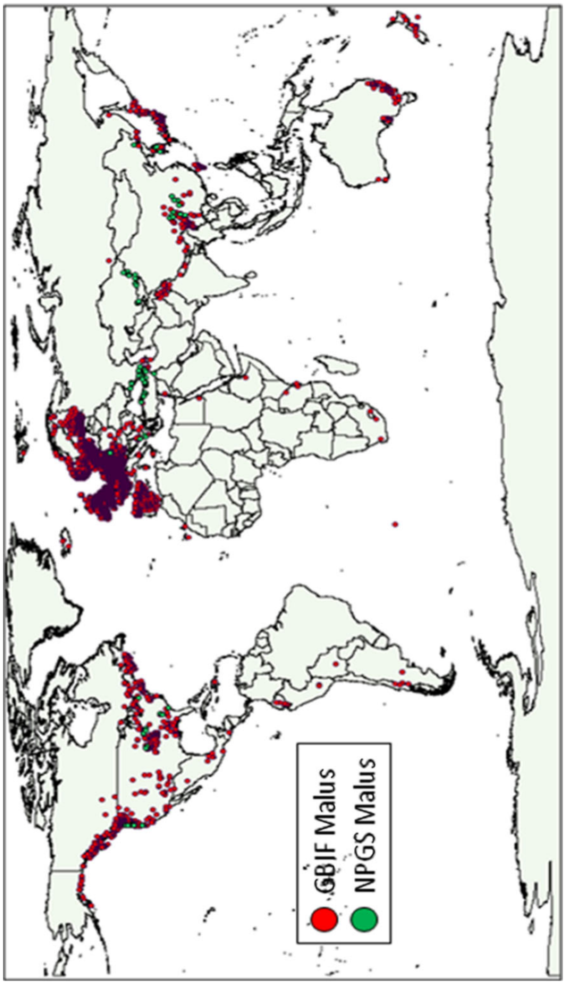

Fig. 2 Distribution of *Malus* accessions listed in the Global Bioinformatics Information Facility (GBIF) with georeferencing data available (*red/purple* points). Data providers include genebanks, botanic gardens, as well as herbaria. Green points illustrate *Malus* accessions with georeference data in the National Plant Germplasm System. (Color figure online)

cost challenges, given the current federal and state funding environments. Advances in genomic technologies, such as available genomic sequences, powerful bioinformatic tools, elucidated marker-trait relationships, and rapid, affordable screening tests have the potential to improve the efficiency, creativity, and productivity of breeding programs. Crop wild relatives can provide breeders and molecular biologists with access to novel alleles that can be incorporated into desirable backgrounds using either traditional crossing or genetic engineering strategies. Future breeding programs will rely on ready access to diverse genetic resources, and international quarantine programs play a key role ensuring that pathogen-free germplasm is imported into the US from other countries.

The USDA-ARS NPGS apple collection provides a world-class repository of apple cultivars and wild relatives. This collection is accessible and is being characterized genetically and phenotypically. Data are publicly available through the GRIN database. Breeders and researchers use the NPGS apple collection extensively, both as germplasm for breeding and as genetic material for fundamental scientific discovery purposes. Novel alleles continue to be discovered and accessed. PGRU scientists are limited by the amount and type of evaluations that can be performed with the current budgets. Given the cost of maintaining large collections, careful consideration must be given as to which new accessions will be accepted into the collection, which are to be maintained and in what form, and which evaluations are the highest priorities. Fingerprinting analyses of the existing diversity will allow for comparisons with other gene bank and arboretum collections from around the world to identify gaps and opportunities; collaborations with international programs may lead to improved accessibility to species that are poorly represented in the NPGS. An understanding of the diversity held in gene banks worldwide will allow for a strategic determination of key *ex situ* populations that must be collected before important sources of wild diversity are lost.

Apples will remain a nutritious fresh and processed food in the human diet. The hard-cider industry is also rapidly growing in the US, providing a new product to a diverse consumer base. Long-term storage and southern hemisphere production ensures that quality fruit are available year-round in the US and worldwide. Both new and traditional breeding techniques are successfully incorporating desirable alleles from novel sources, thus lowering costs, improving resistance, and reducing the need for chemical controls. With a diverse germplasm base secured, this trajectory suggests a positive outlook for the future of apple producers and consumers.

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