Canadian Food Inspection Agency

The Biology of *Malus domestica* Borkh. (Apple)

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Biology Document BIO2014-01: A companion document to Directive 94-08 (Dir94-08), Assessment Criteria for Determining Environmental Safety of Plant with Novel Traits

Photo credit: H. Ardiel

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Ottawa, Ontario
Oct 15, 2013

1. General Administrative Information

1.1 Background

The Canadian Food Inspection Agency's Plant and Biotechnology Risk Assessment (PBRA) Unit is responsible for assessing the potential risk to the environment from the release of plants with novel traits (PNTs) into the Canadian environment. The PBRA Unit is also responsible for assessing the pest potential of plant imports and plant species new to Canada.

Risk assessments conducted by the PBRA Unit require biological information about the plant species being assessed. Therefore, these assessments can be done in conjunction with species-specific biology documents that provide the necessary biological information. When a PNT is assessed, these biology documents serve as companion documents to **Dir94-08: _Assessment Criteria for Determining Environmental Safety of Plants with Novel Traits_**.

1.2 Scope

This document is intended to provide background information on the biology of *Malus domestica*, its identity, geographical distribution, reproductive biology, related species, the potential for gene introgression from *M. domestica* into relatives, and details of the life forms with which it interacts.

Such information will be used during risk assessments conducted by the PBRA Unit. Specifically, it may be used to characterize the potential risk from the release of the plant into the Canadian environment with regard to weediness/invasiveness, gene flow, plant pest properties, impacts on other organisms and impact on biodiversity.

2. Identity

2.1 Name
2.2 Family
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2.4 Common name(s)
2.5 Taxonomy and genetics
2.6 General description

2.1 Name

Malus domestica Borkh. (USDA-ARS 2012).

2.2 Family

Rosaceae (rose family) (USDA-ARS 2012).

2.3 Synonym(s)

Synonyms for *M. domestica* are: *M. malus* (L.) Britton, nom. inval., *M. pumila* auct., *M. pumila* Mill. var. *domestica* (Borkh.) C. K. Schneid., *M. sylvestris* auct., *M. sylvestris* (L.) Mill. var. *domestica* (Borkh.) Mansf., and *Pyrus malus* L. (USDA-ARS 2012).

2.4 Common name(s)

M. domestica is commonly known as apple in English, and pommier commun in French (USDA-ARS 2012).

2.5 Taxonomy and genetics

The genus *Malus* belongs to the rose family (Rosaceae) which includes over 100 genera and 3000 species distributed worldwide, most commonly in temperate regions (Velasco et al. 2010). Species of agronomic importance include: almond, apple, apricot, cherry, peach, pear, plum, quince, raspberry, sour cherry, sweet cherry, and strawberry (Shulaev et al. 2008; Webster 2005a; Westwood 1993) . Other non-edible species with ornamental value include: rose, hawthorn, potentilla, cotoneaster, and pyracantha (Shulaev et al. 2008).

The Rosaceae family has traditionally been divided into four subfamilies on the basis of fruit type. These include: Rosoideae (e.g., *Rosa*, *Fragaria*, *Potentilla*, *Rubus*, fruit an achene, x = 7, 8 or 9); Prunoideae (e.g., *Prunus*, fruit a drupe, x = 8); Spiraeoideae (e.g., *Spirea*, fruit a follicle or capsule, x = 9), and; Maloideae (e.g., *Malus*, *Pyrus* and *Cotoneaster*, fruit a pome, x = 17) (Luby 2003; Shulaev et al. 2008). More recent phylogenetic analyses have resulted in the reclassification of Rosaceae into three subfamilies, namely Dryadoideae (x = 9); Rosoideae (x = 7) and Spiraeoideae (x = 8, 9, 15 or 17), with each of the latter two further divided into supertribes, tribes and subtribes. With less emphasis on fruit type, taxa formerly included in Prunoideae and Maloideae (including apples and pears) were reclassified into Spiraeoideae (Potter et al. 2007; Shulaev et al. 2008). Another recent

nomenclatural change includes the former Maloideae and Spiraeoideae in a new subfamily, Amygdaloideae (see below), based on requirements in the 2012 edition of the *International Code of Nomenclature for Algae, Fungi and Plants* (USDA-ARS 2012; USDA-NRCS 2012). Determination of phylogenetic relationships within the Rosaceae is complex and ongoing but regardless of which classification scheme is used, apples and pears belong to the same subfamily, and along with a handful of other closely related genera, are distinct in having a haploid (x) number of 17 chromosomes (x = 17). They are thought to be of allopolyploid origin, having originated from ancient hybridizations between species in the Prunoideae (x = 8) and the Spiraeoideae (x = 9), followed by chromosome doubling. The original hybrids would have been sterile and only after chromosome doubling would they have formed fertile allopolyploids (Hancock et al. 2008; Luby 2003; Way et al. 1990; Webster 2005a).

Like the family it belongs to, the genus *Malus* is diverse and complex, and there are considerable challenges in species delimitation due to hybridization, polyploidy, and apomixis (Luby 2003). The primary centre of species richness and diversity is in southwest China and Central Asia, with several species ranging eastwards to Manchuria and Japan, and others ranging westwards to Europe (Ferree and Carlson 1987; Ignatov and Bodishevskaya 2011; Luby 2003) . A secondary centre is in North America, with four native species (see Section 5). The number of species included in the genus is still a subject of debate, with different treatments recognizing as few as 8 to as many as 78 primary species, depending on the rank given to certain taxa, and the acceptance of reported hybrids (Hancock et al. 2008; Harris et al. 2002; Jackson 2003; Luby 2003; Rieger 2006; Robinson et al. 2001) . Most species in the genus can be readily hybridized, and many hybrid species, derived naturally or artificially, are recognized (Hancock et al. 2008; Luby 2003). A list of 58 species and hybrid species currently recognized in the taxonomy database of the U.S. Department of Agriculture Germplasm Resources Information Network (GRIN) is provided in Appendix 1. Most apple species are diploid ($2n = 2x = 34$) but higher somatic numbers exist (e.g., 51, 68, 85) and several cultivated types are triploid (Hancock et al. 2008).

The cultivated apple, *M. domestica* (also sometimes designated *M.* x *domestica* Borkh. to indicate its hybrid origin), is thought to be the result of initial domestication followed by inter-specific hybridization (Hancock et al. 2008; Luby 2003; Mabberley et al. 2001; Qian et al. 2010) . It is not a naturally evolved species; rather it has been collected, transported, hybridized and selected by people over millennia (Ferree and Carlson 1987). Its primary wild ancestor is thought to be *M. sieversii* (Ledeb.) M. Roem., whose range is centered at the border of western China and the former Soviet Union (Hancock et al. 2008; Luby 2003). This has been supported by recent genetic analysis (Velasco et al. 2010). Other species which are thought to have contributed to the genetic background of *M. domestica* are: *M. orientalis* Uglitzk. of Caucasia, *M. sylvestris* (L.) Mill. from Europe, *M. baccata* (L.) Borkh. from Siberia, *M. mandshurica* (Maxim.) Kom. ex. Skvortsov from Manchuria, and *M. prunifolia* (Willd.) Borkh. from China. It is likely that these species hybridized with cultivated apples as they were spread by people (Hancock et al. 2008; Juniper et al. 1999). A number of species are also known to have contributed to the *M. domestica* complex in modern breeding programs, including: *M. floribunda* Siebold ex Van Houtte, *M.* x *micromalus* Makino, *M.* x *atrosanguinea* (hort. ex Spath) C. K. Schneid., *M. baccata*, *M. zumi* (Matsum.) Rehder and *M. sargentii* Rehder (Hancock et al. 2008).

Throughout its history of cultivation, more than ten thousand cultivars of *M. domestica* have been developed, although many of these are now lost (Qian et al. 2010; Rieger 2006; Velasco et al. 2010; Way et al. 1990) . Currently, about 100 cultivars are grown commercially, the most popular worldwide including: 'Fuji', 'Delicious', 'Golden Delicious', 'Gala' 'Granny Smith', 'Idared', 'Jonagold', 'Braeburn', 'Cripps Pink', 'Jonathan', 'Elstar' and 'McIntosh' (Belrose 2012; Jackson 2003). The majority of cultivars are diploid (e.g., 'Fuji', 'Delicious', 'Golden Delicious', 'Gala', 'Granny Smith', 'Jonathan', 'McIntosh'), while some are triploid (e.g., 'Jonagold') (Hampson and Kemp 2003; Westwood 1993) and a few are tetraploids (e.g., 'Antonovka Ploskaya', 'Wealthy Tetraploidnyi', 'Papirovka Tetraploidnaya', 'McIntosh Tetraploidnyi') (Sedov and Makarkina 2008).

Taxonomic position (USDA-ARS 2012; USDA-NRCS 2012):

Kingdom: Plantae (plants)
Subkingdom: Tracheobionta (vascular plants)
Superdivision: Spermatophyta (seed plants)

Division: Magnoliophyta (flowering plants)
Class: Magnoliopsida (dicotyledons)
Subclass: Rosidae
Order: Rosales
Family: Rosaceae (rose family)
Subfamily: Amygdaloideae
Tribe: Maleae
Subtribe: Malinae
Genus: *Malus*
Species: *Malus domestica* Borkh.

2.6 General description

M. domestica is a small- to medium-sized, much-branched, deciduous tree with a single trunk and a broadly spreading canopy. Wild trees can reach 10-15 m in height, while cultivated trees are generally 2-5 m tall (in cultivation, tree size and shape are heavily dependant on rootstock and training system) (CABI 2012; Flora of China editorial committee 1959+; Rieger 2006) . Roots consist of a horizontal layer of permanent, thickened, spreading scaffold roots less than 50 cm from the surface, and numerous vertical 'sinkers' descending to an impermeable layer or water table (Jackson 2003). Young stems and twigs are somewhat tomentose (hairy), while older branches are glabrous (smooth) (Bailey and Bailey 1976; CABI 2012; Webster 2005a) . Buds are purplish brown, ovoid and densely hairy (Flora of China editorial committee 1959+). Leaves are alternate, elliptic-ovate, rounded at the base, 4-13 cm long x 3-7 cm wide, with irregularly saw-toothed margins, and usually hairy beneath (CABI 2012; Rieger 2006; Webster 2005a). Flowers are usually terminal on spurs (although they may grow laterally from one year old wood in some cultivars), borne in groups of 4-6, in inflorescences that have variously been described as corymbs, corymbose racemes, cymes, and false cymes (CABI 2012; Jackson 2003; Rieger 2006). Flowers are typically 3-4 cm in diameter, with 5 petals varying from white to deep pink, 5 sepals, about 20 stamens in 3 whorls (10 + 5 + 5) with yellow anthers, and a pistil comprised of five styles united at the base (Figure 1) (Flora of China editorial committee 1959+; Hancock et al. 2008; Jackson 2003). The pedicel and calyx are usually woolly, and the calyx is persistent in the fruit (Webster 2005a). Fruit is an ellipsoid to obovoid globe-like pome indented at the base and usually also at the apex; usually more than 5 cm in diameter and weighing 200-350 grams (Figure 1). It may vary in colour, from uniformly red, green, or yellow, or bi-coloured, such as striped or blushed red on a yellow or green background. Each fruit contains a cortex of (edible) flesh between the skin and the core line, and a central core of fleshy pith with a papery capsule of five fused carpels. Each carpel generally contains two seeds. Seeds are smooth, shiny, and chestnut brown (Jackson 2003; Rieger 2006).

M. domestica closely resembles four other *Malus* species present in Canada (see Section 5), but can be distinguished primarily by its fruit which are significantly larger (6-12 cm in diameter), and by its branches which do not usually have thorns (Gleason and Cronquist 1991) (note that *M. domestica* plants grown from seed may have thorns in their juvenile state). The native crabapple species *M. coronaria* (L.) Mill. and *M. fusca* (Raf.) C. K. Schneid. both have thorny branches; *M. coronaria* has glabrous leaves and hypanthium, pink flowers fading to white with pink or salmon-coloured anthers (as compared to *M. domestica's* white flowers tinged with pink, and yellow anthers), and small fruit (2-3 cm in diameter), while *M. fusca* has yellow to purplish-red fruits about 1 cm in diameter (Gleason and Cronquist 1991; Scoggan 1979). The introduced crabapple species *M. baccata* and *M. prunifolia* both have glabrous pedicels, leaves and hypanthium, and small, tart fruit. *M. baccata* has glabrous twigs, a deciduous calyx, and fruit about 1 cm in diameter, while *M. prunifolia* has pubescent twigs, a persistent calyx, and fruit about 2 cm in diameter (Gleason and Cronquist 1991).

Figure 1: Flowers and fruit of *M. domestica* (Photos by K. Allison and C. Wilson, CFIA)

3. Geographical Distribution

3.1 Origin and history of introduction

M. domestica is thought to have originated in Central Asia where its primary ancestor, *M. sieversii*, isnative to the foothills between western China and the former Soviet Union (Figure 2) (Hancock et al. 2008; Harris et al. 2002; Velasco et al. 2010) . Apples are the main forest tree in this region and *M. sieversii* is widespread in the Tien Shan mountains at elevations of 1200-1800 m (Luby 2003; Velasco et al. 2010). *M. sieversii* is the only wild species that shares all the characteristics of *M. domestica*, in terms of fruit and tree morphology. Its fruits are highly variable and display the full range of colours, forms and tastes found in cultivated apples across the world. Humans have lived and practiced nomadic agriculture in this region for thousands of years, and it is thought that prior to deliberate domestication, there may have been a long period of opportunistic gathering of apples, and unintentional planting of trees via garbage disposal (Hancock et al. 2008; Luby 2003). Bears and other vertebrates may also have contributed to dispersal (Ignatov and Bodishevskaya 2011; Juniper et al. 1999).

Ancient trade routes that linked China to the Middle East and Europe are thought to have facilitated the repeated short- and long-distance dispersal of *M. sieversii* to the east and west from its area of origin in Central Asia (Harris et al. 2002; Velasco et al. 2010). Travellers on foot as well as camels and pack horses are thought to have used parts of the Old Silk Road as early as the Neolithic period (~9000 BC) and the route was well established by the Bronze Age (~2500 BC), providing untold opportunities for the dispersal of fruit and seeds, either intentionally or unintentionally (Hancock et al. 2008; Harris et al. 2002; Luby 2003) . As a result of this movement, hybrids could have occurred to the east with species native to China (e.g., *M. baccata*, *M. mandshurica*, and *M. prunifolia*) and to the west with European species (e.g., *M. orientalis* and *M. sylvestris*)(Hancock et al. 2008; Juniper et al. 1999; Luby 2003).

Archaeological and historical evidence indicates that apples were being collected in the wild during the Neolithic and Bronze ages at sites throughout Europe (Harris et al. 2002; Juniper et al. 1999), and cultivated as early as 3,000 BC in the near East (e.g., Turkey, Syria, Iraq) (Hancock et al. 2008). Writings from the Persian Empire (e.g., Iran and beyond) indicate that apples were widely cultivated there by 500 BC. When Alexander the Great conquered the Persians around 300 BC, the cultivation of fruits was introduced to the Greek world as well, and from there to the Romans (Hancock et al. 2008; Luby 2003). Historical evidence indicates that ancient Greeks were familiar with the art of grafting, and

that Roman horticulturalists used budding, grafting and rootstock techniques. By the first century AD, several apple cultivars were recorded by the Roman writer Pliny (Juniper et al. 1999). The rise of the Roman Empire spread cultivation of the domestic apple north and west into Europe, where it supplanted and hybridized with the native crabapple, *M. sylvestris*. Over the next several centuries, apple cultivation was maintained through the rise and spread of Christianity and Islam, particularly in the abbey gardens of Europe and the orchards of Iberia (e.g., modern day Portugal and Spain) (Hancock et al. 2008; Luby 2003).

By the 1200s, cultivated apples were becoming increasingly popular throughout Europe, in the gardens of both royalty and commoners, and by the 1600s there were at least 120 cultivars of apple described (Luby 2003). In 1826, the Royal Horticultural Society of England recognized at least 1200 varieties, and these were starting to be recognized and classified based on their desirability for different end uses (e.g., cooking apples, dessert apples, cider apples). The late 1800s and early 1900s represent the period of greatest diversity for apple cultivation in Europe, with hundreds of locally popular cultivars being grown in thousands of small orchards, and the known list of cultivars probably exceeding 2500 (Hancock et al. 2008; Juniper et al. 1999; Luby 2003).

In the meantime, European colonists had introduced *M. domestica* to the Americas (1500-1600s), South Africa (1650s), Australia (1788), and New Zealand (1814). By the late 1800s, it had also been introduced to southern and eastern Asia, where it supplanted the Chinese soft apple, *M.* x *asiatica* Nakai, the primary cultivated apple in that region for over 2000 years (Hancock et al. 2008; Luby 2003).

In the Americas, *M. domestica* was first introduced by Spanish priests to missions in Chile and California in the 1500s. Spanish and Portuguese colonists continued to introduce apples to their settlements in the suitable temperate climate zones of Central and South America, and European settlers brought seeds to establish orchards in the eastern parts of the U.S. and Canada. By the 1620s, the first apple orchards were recorded in New England, and likewise during the 1600s, French colonists established orchards in Canada, along the St. Lawrence River valley and in the milder valleys of Nova Scotia and New Brunswick. As settlers moved westwards in North America, apple orchards became a requirement for homesteading, and by the late 1800s apples were grown on the west coast of North America as well (AAFC 2011; Hancock et al. 2008; Luby 2003) . Very hardy cultivars such as the Wealthy were developed in the late 1800s for cold areas of the US great plains (Luby and Fennell 2006). Eventually, a new group of new American cultivars was established, such as 'Jonathan', 'Wagener' and 'Golden Delicious', which were successful in the more extreme American climates and also subsequently did well in South Africa, Australia and the Mediterranean (Juniper et al. 1999).

By the early 1900s, the U.S. and Canada were the two largest apple-producing nations in the world. By the late 1900s, the former Soviet Union was also an important world producer, and by the turn of the (21st) century, China was the largest apple producer, with a large proportion of the crop being exported as concentrated juice. Today, world production of apples exceeds 70 million metric tons, with China, the U.S., India, Turkey, Poland, Italy, France and Iran being leading producers (FAO 2013; O'Rourke 2003). Major southern hemisphere production occurs in Brazil, Chile, Argentina, South Africa, New Zealand and Australia, much of it for export to northern hemisphere countries during their spring and summer (FAO 2013; Hancock et al. 2008; Luby 2003; O'Rourke 2003) . Although there are 6000 regionally important cultivars and land races recognized across the world, global trade is dominated by just a few cultivars; primarily 'Delicious', 'Golden Delicious', 'McIntosh' and 'Jonagold' from North America, 'Braeburn' and 'Gala' from New Zealand, 'Granny Smith' from Australia and 'Fuji' from Japan (Hancock et al. 2008; Luby 2003).

3.2 Native range

The native range of *M. domestica* is difficult to determine, as the species is a product of domestication and multiple hybridizations across the world over thousands of years. Its primary ancestor isnative to the foothills between western China and the former Soviet Union (Hancock et al. 2008; Velasco et al. 2010), and this is suggested by some authors to be its centre of origin (e.g., see discussion in Harris et al. 2002; Robinson et al. 2001).

Asia Possibly native to Kazakhstan, Kyrgystan, Tajikistan, Turkmenistan, Uzbekistan (Harris et al. 2002; Robinson et al. 2001).

3.3 Introduced range

Asia

Cultivated in Afghanistan, Armenia, Azerbaijan, Bhutan, China, India, Indonesia, Iraq, Iran, Israel, Japan, Jordan, Kazakhstan, Korea (Republic of), Kyrgyzstan, Lebanon, Myanmar, Nepal, Pakistan, Philippines, Syria, Tajikistan, Thailand, Turkey, Turkmenistan, Uzbekistan, Vietnam, Yemen (CABI 2012; Flora of China editorial committee 1959+; Hancock et al. 2008) . Production in tropical Asia is limited to high altitudes; in India this includes the temperate North Western Hills region and to a lesser extent the North Eastern Hills region (Papademetriou and Herath 1999).

Africa

Cultivated in Algeria, Egypt, Kenya, Madagascar, Morocco, Reunion, South Africa, Tunisia, Zimbabwe (CABI 2012).

North America

Cultivated in Canada, Mexico, United States (CABI 2012). Also naturalized in Canada and the United States (Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979; USDA-NRCS 2012).

Central America

/ Cultivated in Grenada, Guatemala, Honduras (CABI 2012).
Caribbean

South America

Cultivated in Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Paraguay, Peru, Uruguay (CABI 2012).

Europe

Cultivated in Albania, Austria, Belarus, Belgium, Bulgaria, Croatia, Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Malta, Moldova, Netherlands, Norway, Poland, Portugal, Romania, Russian Federation, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, United Kingdom (CABI 2012; Tutin et al. 1968). Reported throughout Europe as "often escaping and occasionally naturalized" (Tutin et al. 1968).

Oceania

Cultivated in Australia, New Zealand (CABI 2012; Mabberley et al. 2001). Also naturalized in Australia (Australian National Botanic Gardens 2012) and present as a casual exotic in New Zealand (Landcare Research 1996-2012).

3.4 Potential range in North America

M. domestica is cultivated throughout temperate areas of the world, including North America (Mexico, U.S. and Canada). In the U.S., apples are grown in every continental state and commercial production occurs in 35 states, with top producers including Washington, New York, Michigan, Pennsylvania, California and Virginia (Rieger 2006; U.S. Apple Association 2012); *M. domestica* is also reported as naturalized in 41 states (Kartesz 2011; USDA-NRCS 2012). In Canada, *M. domestica* is cultivated in all provinces but not the northern territories, with major production in British Columbia (19%; 3794 ha), Ontario (37%; 7541 ha), Quebec (31%; 6232 ha), New Brunswick (1%; 255 ha) and Nova Scotia (11%; 2226 ha) (AAFC 2011). It is also reportedly naturalized in British Columbia, Manitoba, Ontario, Quebec, New Brunswick, Nova Scotia, and Prince Edward Island (Brouillet et al. 2010+; CFIA and

NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979).

Cold hardiness and length of growing season requirements vary significantly between different cultivars of *M. domestica*, although as a rule of thumb most varieties do best in USDA Plant Hardiness Zones 4-7 (e.g., 'Delicious'; 'Duchess'; 'Gala'; 'McIntosh'; 'Enterprise'; 'Macoun'; 'Wolf River') (Hampson and Kemp 2003; Jackson 2003; Orange Pippin Ltd. 2012; Webster 2005b; Westwood 1993) . Some varieties recommended for use in North America also do well in USDA Plant Hardiness Zone 3, including: 'Honeycrisp', 'Spartan', 'Sunrise', 'Sweet Sixteen' (BCMA 2006; Orange Pippin Ltd. 2012). USDA Plant Hardiness Zones 3-7, which spans from -40°C to -12.3°C average annual minimum temperature, represent about one-third of Canada south of 60° latitude (see map at: http://planthardiness.ars.usda.gov/PHZMWeb/Images/northamerica.jpg).

3.5 Habitat

In general, *M. domestica* is considered best adapted to the cool-temperate zone between about 35-50° latitude, in areas with high light intensity, warm days, and cool nights (Rieger 2006; Webster 2005b). It has a more northern range than many other fruit crops due to its relatively late blooming and cold hardiness (Rieger 2006). It is also grown to a lesser extent in semi-arid, subtropical and tropical areas, where irrigation, altitude, and various cultural strategies are used to overcome climatic limitations (Hampson and Kemp 2003; Westwood 1993). An example of the range of temperatures over which apples are successfully produced is provided by Jackson (2003). At the extremes, the sites presented include Poland, with winter monthly minimum temperatures of -17°C and summer monthly maximum temperatures of 30°C, and Egypt with winter minimums of 1°C and summer maximums of 43°C (Jackson 2003).

The primary climatic constraints for *M. domestica* include inadequate winter chilling in warmer climates, as well as summer heat stress and fruit sunburn (i.e., mild winters and hot summers), and winter freeze damage in more northerly regions (i.e., cold winters) (Jackson 2003). *M. domestica* requires a winter chilling period (about 1000-1600 hours at <7°C) to break dormancy, so winters cannot be too mild. If the dormancy requirement is not met, budbreak is sporadic and light, and cropping is poor. High summer temperatures (e.g., 40°C for more than a few days) can also cause tree stress, as they interfere with the ability to take up and transpire water quickly enough to cool the leaves, and can cause reduced photosynthesis, reduced fruit size and colour, and sunburned fruits (Webster 2005b). Conversely, *M. domestica* can also be damaged by frost, and if frost follows warm temperatures budbreak is accelerated and often premature (Rieger 2006). The level of damage caused by low temperatures is dependent on the stage of dormancy of the trees; trees are most hardy in the middle of winter and more vulnerable in the late fall and early spring. Frost-free springs are particularly important (Webster 2005b). Apple trees begin to harden in the fall from the outer shoots down the trunk, so that buds and shoots are less sensitive to frost injury than roots. Wood and buds of apple trees may be hardy to -40°C but rootstocks can only survive to about -18 °C and open flowers and young fruit can be killed by brief exposure to -2°C or colder (Palmer et al. 2003; Rieger 2006). Frost injury to flowers can reduce fruit yield by as much as 90% (AAFC 2011; Solymar 2004).

Climatic tolerance varies significantly among cultivars of *M. domestica*. For example, 'McIntosh' and 'Antonkova' are considered outstanding for winter hardiness and can withstand the very low winter temperatures of continental climates (e.g., in Canada). By contrast, large-scale production in countries such as Egypt is based on varieties 'Anna' and 'Dorset Golden', which have been selectively bred for warmer climates and require less winter chilling to achieve budbreak (e.g., 500 hours at 7°C) (Rieger 2006).

Another important factor related to climate suitability is length of growing season, and this also varies greatly between cultivars of *M. domestica*. On average, apples reach maturity about 120-150 days after flowering, but some cultivars may mature in as little as 70 days and others may require as long as 180 days (Rieger 2006). Time to maturity varies with temperature (e.g., warmer temperatures reduce time to maturity) so that it varies for a given variety from place to place; however, rankings of "early" or "late" varieties relative to each other are fairly consistent (Jackson 2003). Short-season cultivars tend to have a wide climatic tolerance; they do well in colder, northerly apple-producing regions such as Canada (e.g., 'McIntosh') and may also be grown as early-season crops in countries like New Zealand

and France (e.g., 'Cox') (Jackson 2003). Long -season cultivars like 'Braeburn', 'Fuji', 'Cripp's Pink', and 'Granny Smith' cannot generally be grown successfully in northern areas, and do best in the milder climates of the southern hemisphere (Hampson and Kemp 2003; Jackson 2003).

M. domestica responds positively to sunlight, and increased solar radiation generally results in increased light penetration into the tree canopy, and increased potential for photosynthesis. Cloud cover associated with rainfall is noted as a negative factor reducing the availability of solar radiation in many fruit-growing areas (Jackson 2003). Jackson (2003) provides the range of solar radiation during a 5-month growing season for five different apple-growing areas, with Wilhelminadorp, the Netherlands at 2.50 GJ/m and Davis, California with 4.13 GJ/m at the extremes. Rieger (2006) notes that the red skin colour of the fruit of many varieties is stimulated by sunlight; however overexposure of the fruit to sun can cause sunscald.

M. domestica is relatively drought intolerant, and not suited for cultivation in very arid areas unless abundant supplies of fresh water are available for irrigation (Webster 2005b). In Canada, summer droughts can negatively affect tree health and fruit production, and excessive direct sunlight and a thin ozone layer can also lead to fruit scorch, a phenomenon most often recorded in British Columbia, but also occasionally in Ontario (AAFC 2011). Conversely, high humidity and rainfall are also problematic, as the moisture can promote infections and diseases (e.g., apple scab, fire blight), and heavy rainfall can negatively affect soil structure and aeration. In general, *M. domestica* requires about 50-60 cm of rainfall or irrigation distributed throughout the growing season, and trees grown in drier climates experience less disease pressure (Rieger 2006; Webster 2005b).

M. domestica can be grown in a variety of soil types but performs optimally in deep well-drained, loamy soils with a pH of 6-7 and high organic matter (AAFC 2011; Rieger 2006; Solymar 2004). Sandy soils produce less vigorous growth and require more irrigation, as they have less organic matter and are prone to leaching. Clay soils are higher in organic matter and produce more vigorous growth, but provide poor drainage and are less suitable for root growth (AAFC 2011). Like most fruit crops, *M. domestica* is largely intolerant of poorly drained soils (Rieger 2006). Orchards are often located on hillsides, allowing cool air to flow down the slope, and avoiding spring frosts and waterlogged soil conditions (Webster 2005b). Ideally, the slope should be graded between 4-8 % and face south, for greatest exposure to the sun (AAFC 2011; Webster 2005b).

Outside of cultivation, *M. domestica* has naturalized in many parts of the world, as in North America, where it grows in abandoned pastures, clearings, roadsides, and borders of woods (Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979; Stover and Marks 1998; USDA-NRCS 2012).

4. Biology

4.1 Reproductive biology

M. domestica reproduces naturally by means of seed. Most cultivars rely on pollination to produce fertilized seeds but some cultivars can produce unfertilized (apomictic) seeds (Westwood 1993). Some cultivars can also reproduce vegetatively by root suckering (Hancock et al. 2008; Westwood 1993). The majority of cultivars cannot self-pollinate due to a multi-allelic S-locus (S-RNase) - mediated gametophytic self-incompatibility mechanism (Sassa et al. 1994). Because of this self-incompatibility, the majority of cultivars display high levels of allelic heterozygosity and thus when propagated from seed, are not true-to-type, in that they are extremely variable and generally bear fruits of poor size,

appearance and quality (Webster and Wertheim 2003). Incompatibility genes are sufficiently disparate between cultivars that almost all cultivars are cross-fertile. Much study has gone into this area of research and compatibility lists are generally available (Kemp 1996). For consistent cropping, it is recommended that about 10% of an orchard area be devoted to pollinizer (pollen donor) cultivars. These pollinizer cultivars can be either another compatible apple cultivar or a specialized crabapple pollinizer cultivar (Maggs et al. 1971; Westwood 1993). Crabapples are commonly used as an alternative or additive source of pollen because they are heavy bloomers and provide a large source of compatible pollen. *M. domestica* flowers are predominantly insect-pollinated, mainly by bees when grown as a commercial crop (see Section 4.4). Mature pollen grains have 3 germinal furrows and are rugulate, having folds or wrinkles (Pratt 1988). Pollen grains are large and heavy resulting in very little wind pollination.

Flower development takes roughly 10 months, beginning with the transition from vegetative to reproductive development (late June in the Northern Hemisphere) and ending with anthesis (late April to the beginning of May) in the subsequent year (Dennis 2003; Kotoda et al. 2000). Flowering occurs in early spring when white to deep pink flowers develop in a cyme-like inflorescence of 4-6 flowers. The centre flower which opens first is often referred to as the "king bloom". Most flowers are borne terminally on spurs and less frequently, laterally on long shoots. Flowers borne on short spurs begin the transformation from vegetative buds to flower buds 4-6 weeks before lateral buds (Jackson 2003). The flowers are hermaphroditic with the ovary embedded in the floral cup and flower parts located above the ovary. A normal flower contains five carpels each with two ovules, five sepals, petals and styles and usually 20 stamens (Dennis 2003; Rieger 2006). Flowering can be affected by many biotic (endogenous phytohormones, previous year's crop load, pathogens and pests) and abiotic (light, water stress, nutrients, temperature and exogenously applied chemicals) factors as well as cultural practices including: grafting, pruning, scoring and/or ringing the base of the tree (Jackson 2003).

The stigma produces extracellular secretions which provide a moist environment for pollen deposition and germination (Jackson 2003). Once the pollen grains have germinated, the pollen tubes grow down the style into an ovule where fertilization of the egg cell (to form a zygote) and polar nuclei of the egg sac (to form the endosperm) occur (Dennis 2003). Pollen fertility of most apple cultivars is close to 100% but is reduced in some cultivars, such as 'McIntosh', by unknown factors and in others, such as 'Jonagold', by triploidy. The period of flowering during which viable pollen is produced varies depending on weather conditions and generally lasts from 7 to 30 days. The effective pollination time, the period during which the ovule is capable of being fertilized minus the time required for the pollen tube to grow from the stigma to the ovule, varies from 2 to 9 days (Pratt 1988). Thus the longevity of ovules is a limiting factor in fruit set.

Fruit reach maturity 120-150 days after bloom for most cultivars and weigh about 150-350 grams (Rieger 2006). Fruit development can be divided into three stages: (i) the first 25 days when petals fall, fruit growth is rapid, embryo in the seed develop slowly and growth is predominated by cell division, (ii) the next 50 days (up to 75 days after petal fall) when the embryo develops rapidly and the fruit approaches its final size with growth predominated by cell enlargement, and (iii) the last roughly 14 days (up to 90 days after petal fall) during which the seed testa turns brown and the fruit enlarges slightly, ripens and, in some cultivars, falls (Pratt 1988). In cultivation, about 1 to 5% of apple flowers develop into mature fruit. The others fail because of lack of pollination, competition between fruits or cultural practices (i.e., thinning to promote fruit size and quality and discourage biennial bearing). Biennial bearing results from heavy cropping in one year which acts to inhibit flower bud initiation and reduce flowering in the second year (Jackson 2003). Fruit is picked between early August and late November in north temperate zones and can be stored for up to a year depending on the cultivar. A large, mature, cultivated apple tree can produce in the order of 2000 fruits per year, potentially yielding 10,000 seeds, and may live for 50 years or longer, theoretically producing 500,000 seeds in its lifetime.

4.2 Breeding

Commercial apple trees are composed of genetically distinct portions. The rootstock constitutes the root system including a small portion of the lower trunk, while the scion comprises the majority of the

above-ground tissues, including the fruit bearing portion of the tree. Grafting or budding techniques are typically the process by which the scion is joined to the rootstock (Webster and Wertheim 2003). As mentioned in section 4.1, because cultivars are of a heterozygous nature, fruits resulting from open pollinations bear highly variable seeds and this precludes the propagation of apple cultivars by seed. Instead, the cultivation and maintenance of *M. domestica* cultivars with desirable characteristics relies on vegetative propagation methods such as grafting, layering or other clonal methods rather than seeds (Dennis 2003; Rom and Carlson 1987). The principal reason for the use of rootstocks is for the clonal propagation of desirable cultivars (Webster and Wertheim 2003). There are also other important factors conferred to the grafted tree from the rootstock. Rootstocks can affect the vigour of vegetative growth, fruit size, fruit growth, precocity and yield of the scion portion of the tree. The rootstock can also play a role in the susceptibility of a tree to biotic and abiotic stresses (Webster and Wertheim 2003). As cultivated apple is a composite, some cultivars are bred based on selection of their qualities to the fruiting scion portion and others are developed focusing on the important attributes of desirable rootstock.

Some cultivars are available in various strains, which differ from the original cultivar in growth habit, fruit color or time to maturity. Strains are thought to occur from natural bud mutations in established cultivars that are selected and propagated for improved characteristics. Some cultivars have many strains, for example approximately 250 different strains of Red Delicious have been described and cultivated (Penn State University 2013).

In modern breeding programs, major objectives include increasing the quality or marketability of fruit, reducing production costs and increasing resistance to pests (Hancock et al. 2008; Laurens 1999).

There are several characteristics of *M. domestica* that inhibit rapid genetic improvement of cultivars, most notably: a long juvenile period, large tree size, and self-incompatibility, in conjunction with high allelic heterozygosity and inbreeding depression (Brown and Maloney 2003). The traditional breeding method that is most commonly used is a modified backcross, where a different recurrent parent is used in each generation of backcrossing. This process is laborious and time consuming; for example, it took several decades to successfully introgress a scab resistance trait from crabapple into a commercial cultivar (Gessler and Pertot 2012). Some traits, for instance fruit quality, are affected by many environmental and genetic factors, making breeding efforts towards their development and improvement even more difficult (Brown 2012; Kumar et al. 2012a). Marker-assisted selection is a strategy used in modern breeding programs that employs the use of genetic markers associated with a specific trait to inform the breeding process with the goal of integrating that specific marker/trait into new cultivars. There are several advantages to using a marker-assisted approach over a phenotypic evaluation, namely removing the environmental influences from the screening process and early screening (typically at the seedling stage) which translates into savings in overall breeding costs (i.e., land area requirements, maintenance, field evaluations) (Khan et al. 2012). While marker-assisted selection has been effective in integrating large-effect loci (e.g., red-fleshed fruit) into apple breeding programs (Chagné et al. 2007), it has proved difficult to develop the many traits associated with multiple small-effects genes, so-called quantitative or polygenic traits (Kumar et al. 2012a).

The genome of *M. domestica* was recently sequenced (Velasco et al. 2010). This has led to an increase in trait-marker linkage efforts. Of note, large-scale, multi-year projects aimed at bridging the gap between molecular genetic research and breeding (e.g., RosBREED, Fruit Breedomics Consortium) are currently underway (Fruit breedomics consortium 2012; Iezzoni et al. 2010), and significant implications for genetic improvement have already been reported. Chagné et al. (2012) used genomic sequence data from 27 globally important apple cultivars (produced by RosBREED) for the development of a broad coverage single nucleotide polymorphism (SNP) array (Chagné et al. 2012), and assembly of other SNP arrays has also been reported (Khan et al. 2012). Development of such tools allows for novel methods of genetic improvement, such as Genomic Selection, a statistical approach to estimate breeding potential. Genomic Selection has been effective at directing breeding for complex polygenic traits (Jannink et al. 2010) and has recently been successfully used to direct fruit quality trait breeding in apple (Kumar et al. 2012b).

Recent developments using transgenic approaches are addressing some of the breeding bottlenecks. Successful reduction of the juvenile period was reported using a transgenic approach (Flachowsky et al.

2007). Integration and constitutive expression of the *mads4* gene from silver birch resulted in a significant decrease in age at flowering, with transformed tissue flowering in tissue culture and a generational turnover of one year. The usefulness of this early-flowering trait in expediting plant breeding was further demonstrated by using a marker-assisted approach to increasing resistance to pyramid fire blight, apple scab and powdery mildew over a very short two year span (Flachowsky et al. 2011). This technology is currently being implemented as a tool to reduce trait introgression time for cultivar development by the Fruit Breedomics Consortium (Fruit breedomics consortium 2012). Another recent targeted gene transfer approach to breeding involved the development of marker-free scab resistance events in the non- resistant cultivar 'Gala' (Vanblaere et al. 2011). This study is significant because the research was designed using a cisgenic approach, the first successful report of such an approach in any crop. Cisgenic differs from transgenic recombinant DNA technology, in that the entirety of the introduced genes (including the flanking regions, promoter, introns, exons and terminator sequences in sense orientation) are derived from a crossable donor plant, in this case from *M. floribunda*, a species of crabapple that shows natural resistance to some strains of the apple scab fungus (Vanblaere et al. 2011).

4.3 Cultivation and use as a crop

The majority of trees planted in commercial apple orchards are produced in specialized fruit tree nurseries. However, there are some growers who produce their own nursery trees. Rootstocks may be chosen that reduce the vigour of the scions, although the ultimate size of a cultivated apple tree at maturity is also influenced by the inherent vigour of the scion as well as environmental conditions and pruning (Webster and Wertheim 2003). Trees are generally considered standard (100%), semi-dwarf (60 to 85% of standard size) or dwarf (20 to 50% of standard size) (Parker 1993). The advantages of dwarf trees are that they can be planted at higher densities, trained, pruned and harvested from the ground, have greater pesticide application efficiency and produce fruit earlier than standard trees, which is appealing to growers as there is an increased economic benefit from earlier production (Parker and Unrath 1998). In Canada, there has been a shift towards planting high density commercial apple orchards over the last decade (AAFC 2012). There is more initial cost and labour associated with high density orchards, as the smaller branch framework of the dwarf trees cannot support the heavy crop. To overcome this, a number of different support/training systems have been developed including wooden props, super spindle, slender spindle, vertical axis and vertical trellis (Parker and Unrath 1998; Sanders 1994; van Dalfsen 1989) . Although the general trend in recent years is high density planting of dwarf trees, some semi-dwarf and standard trees are still planted in areas where the climate and soil conditions are unsuited to dwarfing rootstock (Webster and Wertheim 2003). In Canada, apple trees are typically planted in the spring, at densities of 150 to 250 trees/acre for standard trees to densities of 500 to 2000+ trees/acre for dwarf trees, depending on the rootstock and the type of training system used (Parker and Unrath 1998; Sanders 1994; van Dalfsen 1989) . In addition to rootstock and training system, there are a number of other factors that are considered when planting an orchard, including main cultivar and pollinating cultivar(s), soil type and fertility, irrigation, soil drainage, and the spacing between rows of trees as well as between trees in a row.

Trees must transition from a juvenile phase to an adult phase in order to flower and bear fruit. There are several physiological and morphological characteristics that define the juvenile phase including: glabrous, lobed leaves, creeping stems, thorny stems, semi-evergreen nature (in deciduous species), ease of rooting of stems, and less ribonucleic acid in their tissues (Westwood 1993). Mature grafts or buds are typically used for scion propagation and the subsequent vegetative growth consists of mature phase tissue (Westwood 1993). However, newly planted nursery trees undergo a non-flowering phase known as the vegetative adult phase (Westwood 1993). The type of rootstock used has a direct effect on the precocity of the scion portion, though the exact mechanism by which this process occurs is still uncertain (Webster and Wertheim 2003). Scions on dwarfing rootstocks begin to bear fruit approximately 2 to 4 years after planting, scions on semi-dwarfing rootstocks at approximately 2 to 6 years after planting and scions on vigorous rootstocks at approximately 6 to 10 years after planting (Parker 1993). Although no commercial crop is produced during the adult vegetative phase, there are still a number of agronomic issues that must be properly managed to ensure good tree growth including nutrition (through fertigation or soil application), pest control, irrigation, weed control and pruning (Sanders 1994).

M. domestica is a very labour intensive, highly managed crop, especially when the orchard has reached maturity and is ready for commercial production. Table 1 outlines the highlights of a typical management schedule for apple production in Canada.

Table 1. Highlights of a typical management schedule for apple production in Canada (adapted from (AAFC 2011)).

▶ Descriptive text:

Time of Year	Action
Winter - dormancy (December to late April)	• dormant prune trees • apply nitrogen and zinc sulphate • apply dormant spray for pests
Spring - green tip to fruit set (late March to May)	• prune and train trees • place bees in fields when blossom begins • apply chemical thinners • apply soil nutrients • monitor and control pests (insects and diseases) • monitor and control weeds
Summer - fruit growth (June to August)	• summer prune and train trees • apply nutrient sprays (including calcium) • monitor and control pests (insects and diseases) • monitor and control weeds
Fall - harvest period (September to November)	• harvest apple

The average life expectancy of a commercial high-density apple orchard is less than 20 years, although many orchards do maintain an adequate level of production beyond this age (Nova Scotia Department of Agriculture 2009; H. Ardiel, pers. comm.). The life expectancy of a commercial orchard is dependent on a number of factors, such as tree health, apple cultivar, soil quality, environmental location (i.e., heat units, winter injury), market opportunities etc. Changes in consumer preferences for certain apple varieties may also play a role in the decision to replant an orchard.

Fresh fruit is the primary use of cultivated apple in Canada and worldwide (AAFC 2011; Jackson 2003; O'Rourke 2003). Once harvested, the fruit can be stored in controlled atmosphere storage for up to a year (Janick et al. 1996). Apples are also used for juice and juice concentrate, alcoholic cider, fresh apple slices, pie filling, apple sauce, fruit leather, dehydrated fruit bars and other products. By-products of manufacturing, such as pomace left over from juice production, may be fed to livestock, wild animals or used as a food ingredient in, for example, baked goods, for extraction of ester flavours, etc. The apple fruit is notable for its nutritional qualities. It is a natural snack food with low fat content and sugar content of 11-16%; it is also a good source of potassium and soluble fibre, including pectin and other complex carbohydrates and phenol antioxidants (Vinson et al. 2001). There is evidence that regular consumption of apples as part of a healthy diet may aid in the maintenance of good health and prevention of chronic disease (Boyer and Liu 2004).

In Canada, apple fruit from commercial orchards is marketed locally, nationally and internationally. In 2010, the total marketed production of apples in Canada was 336, 834 metric tonnes (mt) (AAFC 2012).

In 2010, Canada exported 25, 969 mt of fresh apple fruit to various countries including the United States (81%), United Kingdom (7%), Mexico (6%) and Taiwan (5%) (AAFC 2012). In 2010, Canada imported 191, 714 mt of fresh apple fruit from the United States (79%), Chile (13%), New Zealand (4%), China (2%) and South Africa (1%).

4.4 Gene flow during commercial fruit production

Insects, most notably honeybees but also bumblebees, other wild bees and to a lesser extent some flies, are the primary vectors for pollination in commercial apple orchards as apple pollen is heavy and not easily carried by the wind (Dennis 2003; Jackson 2003). In apple orchards, the majority of honeybee foraging flights are between flowers on the same tree and secondarily between adjacent trees in the same row and to a lesser extent across rows (Free 1966; Free and Spencer-Booth 1964). Growers typically rent honey bees while an orchard is in bloom, and it is recommended that they be placed at a density of four or five strong colonies per hectare in a mature orchard (Dennis 2003).

Within a commercial orchard, it is recommended that a small percentage (about 10%) of the trees are of a different, compatible cultivar to ensure sufficient availability of suitable pollen required for fruit set (Westwood 1993). Spacing of these pollinizer trees in the orchard can vary, being planted as entire rows, interspersed trees or grafts. If pollinizer trees are unable to produce an adequate supply of pollen, pollen may alternatively be introduced by placing flowering branches, also known as bouquets, from other cultivars throughout the orchard.

Pollen transfer has been studied both for optimizing the layout of an orchard (Kron et al. 2001; Maggs et al. 1971; Wertheim 1991) and to assess the potential for gene flow in *Malus* spp. (Larsen and Kjær 2009; Reim et al. 2006; Soejima 2007; Tyson et al. 2011) . Maggs et al. (1971) found that in a solid-block planted orchard of the 'Granny Smith' cultivar supplied with flowering bouquets of a compatible pollen source, the maximum pollination range was roughly 12 m from the pollen source. Using the 'Baskatong' cultivar, which carries a dominant gene for red leaf colour, Wertheim (1991) monitored gene flow in apple orchards by observing the percentages of red leafed seedlings borne from trees at increasing distances from the 'Baskatong' pollinizer. Findings from this study suggest that the majority of cross-pollination occurs within 15 m from the pollinizer tree. A similar approach, using red leaf colour as a marker to monitor gene flow in an orchard-like scenario, was taken by Reim et al. (2006) who determined that 69% of seeds fertilized by pollen donor plants occurred within the first 10 m and 91% of seeds fertilized by the pollen donor plants occurred within 60 m of the pollen donor plants. Also using a red-leaf screening approach to monitor gene flow in an apple orchard setting, Soejima (2007) determined that roughly 65% of seeds fertilized by pollen donor plants occurred within 8 m and roughly 95% of seeds fertilized by pollen donors occurred within 60 m of the pollen donor tree.

In a survey of a wild population of the crabapple *M. sylvestris*, Larsen and Kjaer (2009) used microsattelite loci data in conjunction with spatial distances of the individual trees in the population to monitor pollen movement in a natural environment. These authors found that successful pollination occurred mostly between nearby trees, with a median distance of about 23 m (Larsen and Kjær 2009). Kron et al. (2001) used allozyme markers to determine parentage of seeds in an effort to track pollen flow in orchards. An allozyme marker from the cultivar 'Idared' was chosen to screen seeds from open pollinated fruit resulting on other cultivars at increasing distances from the 'Idared' cultivar rows. Pollen dispersal generally declined with increasing distance, with 50% of the total seeds sired by 'Idared' occurring within the first four rows, or roughly 20m (Kron et al. 2001).

Monitoring for beta-glucuronidase (GUS) activity in seeds borne from trees located at increasing distances from a row of transgenic GUS-expressing 'Gala' trees was used to track pollen flow in an orchard setting (Tyson et al. 2011). These authors found that 95% of the transgenic seeds observed were found within 15 m of the transgenic row of apples (Tyson et al. 2011). Taken together, these data suggest that the majority of cross-pollination in commercial apple orchards occurs between receptive flowers and proximate pollen sources; however some of these studies have also observed pollen flow at much greater distances. Pollen dispersal distances were reported up to 40 m (Wertheim 1991), 86 m (Kron et al. 2001), 104 m (Reim et al. 2006), 137 m (Tyson et al. 2011) and 150 m (Soejima 2007) in orchard settings, and almost 300m (Larsen and Kjær 2009) in natural settings. In-hive transfer of viable pollen between bees foraging in geographically distant areas may explain long-range pollen flow

(DeGrandi-Hoffman et al. 1986).

In all of these aforementioned studies, distance from the pollen source was a significant factor affecting pollination. Other important factors include weather, pollinator presence, cultivar compatibility and flowering synchrony (Kron et al. 2001). Tyson et al. (2011) have developed a mechanistic model, informed from the transgenic-GUS pollen flow data, to predict bee-vectored pollen transfer. The authors further use the model to examine the effect of buffer rows and isolation distances on outcrossing rates. The model demonstrates that the level of outcrossing is affected by the relative sizes of the transgenic and conventional orchards. As the size of the conventional orchard becomes smaller relative to the transgenic orchard, the isolation distance required to limit the frequency of outcrossing is increased. Furthermore, incorporation of buffer rows between the two orchard types generally reduces the isolation distance required in order to limit outcrossing frequency (Tyson et al. 2011).

4.5 Cultivated *Malus domestica* as a volunteer weed

M. domestica is not regarded as a weedy species although seedlings can be persistent and the species has escaped cultivation and naturalized in both the U.S. and Canada (Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979; Stover and Marks 1998; USDA-NRCS 2012). Generally, volunteer plants originating from seed in apple orchards are very rare due to the perennial nature of the crop and associated orchard management practices, including herbicide treatment of the tree row and mowing of the alley between rows. In a study conducted in New York state, *M. domestica* was reported to be a successional species in abandoned pasture but not in abandoned cultivated fields (Stover and Marks 1998).

4.5.1 Cultural/mechanical control

M. domestica, both in commercial orchards and in feral populations, can be removed by cutting at the base of the stump. The roots must be killed by physical removal of the stump in order to prevent regeneration through suckering.

4.5.2 Chemical control

Similarly to the cultural method mentioned above, apple trees can be removed by cutting at the base of the stump. In order to eliminate re-growth, a herbicide is applied to the exposed cambium area of the stump.

Typically in commercial orchards, herbicide is applied to the tree row to control weeds that would compete with the tree roots for moisture and nutrients. This herbicide application would also control any volunteer apple that may have germinated. There are different herbicide options, comprising different modes of action, available for use in commercial apple production (for a more detailed list, refer to Table 13 in AAFC (2011)).

4.5.3 Integrated weed management

Integrated weed management (IWM) incorporates mechanical, chemical and cultural weed control methods to achieve optimal crop yields (Swanton and Weise 1991). As volunteer apple trees are not a concern in commercial production, IWM methods have not been developed for control.

4.5.4 Biological control

Volunteer apple trees are not a concern in commercial production, thus methods of biological control for apple have not been developed.

4.6 Means of movement and dispersal

The main means of movement and dispersal of apple seeds in natural settings is through frugivorous mammals, such as bears, foxes and deer (Myers et al. 2004; Willson 1993), as well as birds (Witmer 1996). The seeds are small enough to sometimes avoid mastication during consumption by white-tailed

deer and can pass unaffected through the digestive system and remain germinable (Myers et al. 2004). White-tailed deer travel a range of many hectares on a daily basis and are considered dispersers of low numbers of apple seeds (Myers et al. 2004; Williams and Ward undated) (see Figure 2). Aside from the natural means of movement and dispersal, apple seeds are dispersed by humans as a result of the sale of marketable fruit.

Figure 2: White-tailed deer consuming apples in Ontario (Photo Credit: G. Thurston, CFIA).

5. Related Species of *Malus domestica*

[5.1 Inter-species/genus hybridization](#)
[5.2 Potential for introgression of genetic information from *Malus domestica* into relatives](#)
[5.3 Summary of the ecology of relatives of *Malus domestica*](#)

As mentioned earlier, the number of species in the genus *Malus* varies widely, with different taxonomic treatments recognizing anywhere from 8 to 78 primary species (see Section 2.1). Many of the crabapple species can be difficult to differentiate due to the lack of distinguishing characters (Dickson et al. 1991).

Within Canada, there are two native species: the sweet crabapple, *M. coronaria*, native to Ontario, and the Oregon or Pacific crabapple, *M. fusca*, native to British Columbia. In addition, there are three introduced species that are considered naturalized in Canadian floras: the Siberian crabapple, *M. baccata*, the plum- or pear-leaved crabapple, *M. prunifolia*, and the cultivated apple, *M. domestica* (often listed under synonyms *M. pumila* auct.; *M. sylvestris* auct., *Pyrus malus* L.) (Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Duncan and Duncan 1988; Kartesz 1999; Scoggan 1979; Sudworth 1967; USDA-NRCS 2012) . The distribution of these species in Canada is shown in Table 2.

Table 2: Provincial distribution of *Malus* species present in Canada outside of cultivation (from: Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979).

▶ Descriptive text:

Species	Nativity	Distribution by province
Malus baccata (L.) Borkh.	Introduced	ON, QC, NB, NS, ?NL
Malus coronaria (L.) Mill.	Native	ON
Malus domestica Borkh.[1]	Introduced	BC, MB, ON, QC, NB, NS, PE, ?NL

Malus domestica Borkh.			
Malus fusca (Raf.) C. K. Schneid.	Native	BC	
Malus prunifolia (Willd.) Borkh.	Introduced	NB, NS	

1   Distribution collated from reports of synonyms *Malus pumila* Mill. and *Malus sylvestris* (L.) Mill. in the literature.

In the United States, there are two additional native species, the southern crabapple, *M. angustifolia* (Aiton) Michx. and the prairie crabapple, *M. ioensis* (Alph. Wood) Britton, as well as 14 additional introduced species and hybrids that are reported in floras: *M. × arnoldiana* (Rehder) Sarg. ex Rehder, *M. × dawsoniana* Rehder, *M. floribunda*, *M. halliana* Koehne, *M. hupehensis* (Pamp.) Rehder, *M. × magdeburgensis* Hartwig, *M. mandshurica*, *M. × platycarpa* Rehder, *M. sargentii*, *M. × soulardii* (L. H. Bailey) Britton, *M. spectabilis* (Aiton) Borkh., *M. sylvestris*, *M. toringo* (Siebold) de Vriese, and *M. zumi* (Kartesz 1999; Kartesz 2011; USDA-ARS 2012; USDA-NRCS 2012).

In addition, there are a large number of species that are grown and traded for ornamental purposes in North America (Bailey and Bailey 1976), as well as several crabapple species that are grown as pollen donors in commercial apple orchards (Kron and Husband 2007). An online search of nursery databases indicates that, in addition to *M. domestica*, many other species are commonly available at wholesale and retail nurseries in the U.S. and Canada, including: *M. angustifolia*, *M. baccata*, *M. coronaria*, *M. floribunda*, *M. fusca M. hupehensis*, *M. ioensis*, *M. kansuensis* (Batalin) C.K. Schneid*.*, *M. × micromalus*, *M. mandshurica*, *M. × purpurea* (A. Barbier) Rehder*, M. × robusta* (Carriere) Rehder, *M. sargentii*, *M. sikkimensis* (Wenz.) Koehne ex C. K. Schneid., *M. sylvestris*, *M. tschonoskii* (Maxim.) C. K. Schneid., and *M. zumi* (Isaacson and Allen 2007).

5.1 Inter-species/genus hybridization

Most species in the genus *Malus* can be readily hybridized (Hancock et al. 2008; Luby 2003). The capacity for inter-species hybridization within the genus *Malus* is evident by the numerous named hybrids among *Malus* spp. (e.g., Korban 1986; Schuster and Büttner 1995) (see also Appendix 1). The majority of *Malus* spp. are diploid and inter-fertile, as there are no apparent physiological or genetic barriers (Korban 1986). Reports of natural hybrids are common and artificial interspecific hybrids are easily produced (Luby 2003). *M. domestica*, which is thought to be of hybrid origin (Korban 1986), is able to interbreed with its congeners in the genus *Malus* (Korban 1986; Kron and Husband 2009). Interest in controlled hybridization for the improvement of cultivated apples dates back to the 1700s, and reports of successful experimental interspecific hybridizations began in the late 1800s (Korban 1986). Since then, interspecific hybridization has played a major role in genetic improvement and a large number of crosses have been made among *Malus* spp. in research and breeding programs throughout the world, primarily to improve the cultivated apple or to develop new hybrid species with distinctive characteristics (Korban 1986). A list of experimental interspecific hybrids that have been documented in the genus *Malus* is provided by Korban (1986), and includes about 60 different species combinations. Those involving species known in Canada are provided in Table 3 (for the full list see Korban 1986).

Table 3: Reports of experimental interspecific hybrid crosses reported for *Malus* species present in Canada.
▶ Descriptive text:

Cross		Description	References
Female	**Male**		
Malus baccata	**Malus domestica**	2864 pollinations; 840 fruits matured	(Crandall 1926; Korban 1986)

Malus baccata	**Malus prunifolia**	No data	(Korban 1986)
Malus coronaria	**Malus domestica**	54 pollinations; 5 fruits matured	Crandall 1926; Korban 1986)
		19 pollinations; 10 fruits matured	(Kron and Husband 2009)
Malus domestica	**Malus baccata**	734 pollinations; 113 fruits matured	Crandall 1926; Korban 1986)
Malus domestica	**Malus coronaria**	22 pollinations; 0 fruits matured	Crandall 1926; Korban 1986)
Malus domestica	**Malus fusca**	No data	(Korban 1986)
Malus domestica	**Malus prunifolia**	1234 pollinations; 313 fruits matured	Crandall 1926; Korban 1986)
Malus fusca	**Malus domestica**	117 pollinations; 11 fruits matured	Crandall 1926; Korban 1986)
Malus prunifolia	**Malus baccata**	No data	(Korban 1986)
Malus prunifolia	**Malus domestica**	181 pollinations; 54 fruits matured	Crandall 1926; Korban 1986)

Outside of the genus *Malus*, the potential for natural hybridization with other genera appears to be limited. While there has been extensive intergeneric hybridization reported among closely related taxa (e.g., in the former subfamily Maloideae), a summary presented by Robertson et al. (1991) indicates no intergeneric crosses involving *Malus* spp. outside of breeding programs. A reported *Malus × Chaenomeles* hybrid was subsequently discounted by Rudenko (1976, cited in Robertson et al. 1991), and a proposal that the species *M. florentina* (Zuccagni) C. K. Schneid. was the product of hybridization between *Malus* and *Sorbus* sect. *Torminaria* (called ×*Malosorbus*) was also subsequently challenged by several authors who considered it a relictual species of *Malus* (e.g., Huckins 1972, cited in Robertson et al. 1991). This has been further supported by recent taxonomic work (Qian et al. 2008).

Breeding programs have produced intergeneric hybrids between apple and pear (*Malus × Pyrus*) and apple and hawthorn (*Malus × Crataegus*) as reported in Robertson et al. (1991), however these have been met with many difficulties and successful intercrosses relied on techniques such as embryo rescue (Banno et al. 2003). Forced intergeneric hybridization of *Cydonia* (quince)with *Malus* results in fertile genotypes which have been identified as an artificial hybrid genus ×*Cydomalus,* though the seedlings produced are generally weak and of low viability and germinability (Bell and Leitão 2011).

5.2 Potential for introgression of genetic information from *Malus domestica* into relatives

There does appear to be potential for gene introgression from *M. domestica* into its congeners in Canada, although the extent to which this might happen is still unclear. A study conducted by Kron and Husband (2009) in southern Ontario examined populations of the introduced diploid *M. domestica* and the native tetraploid crabapple *M. coronaria*, and found that their geographic ranges and flowering times overlapped sufficiently for cross-pollination to occur. In addition, 27.7% of seed from open-

pollinated fruit was found to be of hybrid origin. This suggests that inter-crossing does happen in natural populations, and that there is potential for gene flow from domestic apples into native crabapple populations. However, the ability of the resulting hybrid plants to survive and backcross with *M. coronaria* is unknown at this time, and the adult trees within the populations were all identified to be distinct species (either *M. domestica* or *M. coronaria*).

This correlates with a number of European studies, which have suggested that the gene pools between wild and cultivated *Malus* spp. remain fairly distinct when feral *M. domestica* trees are present in native *Malus* populations (Coart et al. 2006; Coart et al. 2003; Larsen et al. 2006; Larsen et al. 2008) . These studies used molecular and other analyses on adult trees from natural populations and showed that hybridization between *M. domestica* and native *Malus* species is possible but occurs at low frequencies. Coart et al. (2006) evaluated hybridization between *M. domestica* and the European wild crabapple *M. sylvestris* by looking at nuclear microsatellites from a large sample of trees, the majority from Belgian forests, and found that 11% of the sampled *M. sylvestris* trees were of hybrid origin (Coart et al. 2006). In the case of Larsen et al. (2008), the study also investigated reproductive success of hybrid seed originating from handmade interspecific crosses between *M. domestica* and *M. sylvestris*, measuring fruit set, seed production, germination percentages of resulting seeds and subsequent seedling development. Results showed that interspecific hybridization yielded viable seeds which exhibited normal growth and development up to young seedlings and the authors note that it could be expected that substantial hybridization will occur given the overlap in geographical distribution and flowering time of the two species. However, the authors also note that the lack of observed hybrid individuals in natural populations suggests the possibility of some other type of reproductive barrier operating to maintain genetically distinct populations (Larsen et al. 2008). The nature of this potential barrier is unknown at this time.

5.3 Summary of the ecology of relatives of *Malus domestica*

There are four *Malus* species present in Canada in addition to *M. domestica* (see Section 5). Two of these are native to North America (*M. coronaria* and *M. fusca*), while the other two are introduced (*M. baccata* and *M. prunifolia*) (Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979; USDA-NRCS 2012).

M. coronaria (sweet crabapple) occurs in eastern North America, with a range that corresponds to the Carolinian forest zone (Kron and Husband 2009; Little 1979). It is considered "uncommon to common" within this zone (Little 1979). It is reported from 23 U.S. states bordered by Kansas and Wyoming in the west and Alabama and Georgia in the south, continuing up the eastern seaboard to New York, Michigan and Wisconsin in the north (USDA-NRCS 2012). In Canada, it is at the northern edge of its range, and is present only in southern Ontario (CFIA and NRCan/CFS 2011+; Kron and Husband 2009). Its habitat is described as "low ground, thickets, and clearings" (Scoggan 1979) and "woods and thickets" (Gleason and Cronquist 1991). In Ontario, it occurs in areas that have been subject to European farming practices for at least 200 years, and where feral populations of *M. domestica* are common (Kron and Husband 2009). Today, about half of its range falls within major commercial fruit-growing regions, and in about two thirds of this area *M. domestica* is the primary fruit crop (Kron and Husband 2009).

M. fusca, the Oregon or Pacific crabapple, occurs in western North America with a range that includes California, Oregon and Washington, as well as coastal British Columbia and southern Alaska (Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979; USDA-NRCS 2012) . It is adapted to wet, often disturbed habitats, described as "moist woods, streambanks, swamps and bogs" (Scoggan 1979) and "moist to wet, open forests, streambanks, upper beaches, shoreline thickets, estuary fringes, swamps and bogs in the lowland zone" (E-Flora BC 2012). In British Columbia, it is common on coastal islands and the adjacent mainland (E-Flora BC 2012).

M. baccata, the Siberian crabapple, is introduced in North America and has spread from cultivation to become established in the northeastern U.S. and Canada (Scoggan 1979; USDA-NRCS 2012). It is reported from 13 northeastern U.S. states, from Minnesota and Missouri in the west to Kentucky in the south, Massachusetts on the east coast, and Maine, New York and Michigan in the north (Kartesz 1999; USDA-NRCS 2012). In Canada, it is reported from Ontario, Quebec, New Brunswick, Nova Scotia, and

possibly Newfoundland and Labrador (Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979; USDA-NRCS 2012) . It occurs in thickets and clearings, and along the banks of rivers and old abandoned railways (Scoggan 1979).

M. prunifolia, the plum- or pear-leaved crabapple, is also introduced in North America and like *M. baccata*, has spread from cultivation to become established in the northeastern U.S. and Canada (Scoggan 1979; USDA-NRCS 2012). It has a similar range in the U.S., reported from 13 states from Minnesota to South Carolina, up to Massachusetts on the east coast, and Maine, New York and Michigan in the north (Kartesz 1999; USDA-NRCS 2012). In Canada, it is reported from New Brunswick and Nova Scotia (Brouillet et al. 2010+; CFIA and NRCan/CFS 2011+; Kartesz 1999; Scoggan 1979; USDA-NRCS 2012) . It occurs along roadsides, and in thickets and riverbanks (Scoggan 1979).

6. Potential Interaction of *Malus domestica* with Other Life Forms

M. domestica is susceptible to a number of plant diseases and insect pests. The most economically important disease of apples in North America is apple scab (Jones and Aldwinckle 1990) caused by the fungal pathogen, *Venturia inaequalis* (Cooke) Wint. Apple scab is reported as having widespread yearly occurrence with high pest pressure in all major apple production regions within Canada (AAFC 2011; BCMA 2012). Another significant disease reported as having widespread yearly occurrence with high pest pressure (in Ontario) is fireblight caused by the bacterium *Erwinia amylovora* (Burrill) Winslow et al., which can, under the right conditions, wipe out entire orchards within a growing season (AAFC 2011). Other significant diseases reported as having localized yearly occurrence with high pest pressure or widespread sporadic occurrence with high pest pressure in Canada include black rot (in Ontario), caused by the fungal pathogen *Botryosphaeria obtusa* (Schwein.) Shoemaker, powdery mildew (in Ontario and British Columbia), caused by the fungal pathogen *Podosphaera leucotricha* (Ellis & Everh.) E.S. Salmon, replant disease complex (in Nova Scotia, Quebec and British Columbia), a combination of fungal and bacterial soilborne organisms, as well as nematodes, which affects newly planted apples in locations previously planted as apple orchards (AAFC 2011).

Apple maggot, *Rhagoletis pomonella* (Walsh) and codling moth, *Cydia pomonella* (L.) are serious insect pests for apple each with the potential to cause 100% yield loss and are both reported as having widespread yearly occurrence with high pest pressure for eastern Canadian apple producing regions (Nova Scotia, Quebec and Ontario) (AAFC 2011). Other significant insect pests reported as having widespread yearly occurrence across the major apple producing regions in Canada include: plum curculio, *Conotrachelus nenuphar* (Herbst) in Ontario and Quebec, oblique banded leaf roller, *Choristoneura rosaceana* (Harris) in British Columbia, Ontario and Quebec, three lined leaf roller, *Pandemis limitata* (Robinson), fruit tree leaf-roller, *Archips argyrospila* (Walker), European red mite, *Panonychus ulmi* (Koch) and two-spotted spider mite, *Tetranychus urticae* (C.L.Koch) in Quebec and mullein plant bug, *Campylomma verbasci* (Meyer-Dür) in British Columbia (AAFC 2011). Chemical, biological and cultural control methods are used to limit or eradicate disease and insect pests on apple (AAFC 2011).

Some vertebrates can also be considered pests to apple growers. Birds can become a nuisance by pecking holes in the fruit or wood (AAFC 2011). Various mammals, including rodents, rabbits and deer have been associated with various damage to tree tissues including girdling of bark and feeding on young branches, leaves and buds (AAFC 2011). Bears will also eat the fruit and can damage trees in doing so.

For a list of species associated with *M. domestica*, please refer to Table 4.

Table 4a: Examples of potential interactions of *Malus domestica* with Fungi during its life cycle in a natural environment.

Other life forms	Interaction with *M. domestica* (pathogen; symbiont or beneficial organism; consumer; gene transfer)	Presence in Canada	Reference(s)

	(...transfer)	Canada	
Alternaria alternata (alternaria rot)	Pathogen	Present	(Farr and Rossman undated; Jones and Aldwinckle 1990)
Botryosphaeria spp. (white rot, black rot)	Pathogen	Present	(AAFC pathology database undated; Jones and Aldwinckle 1990)
Botrytis cinerea (dry eye rot; grey mold)	Pathogen	Present	(AAFC pathology database undated; Brown 2012; Jones and Aldwinckle 1990)
Colletotrichum gloeosporioides (bitter rot) (= *Glomerella cingulata*)	Pathogen	Present	(Farr and Rossman undated; Jones and Aldwinckle 1990)
Gloeodes pomigena (sooty blotch and flyspeck)	Pathogen	Present	(Farr and Rossman undated)
Gymnosporangium juniperi-virginianae (cedar apple rust)	Pathogen	Present	(Farr and Rossman undated; Jones and Aldwinckle 1990)
Mucor piriformis (mucor rot)	Pathogen	Present	(Farr and Rossman undated)
Mycorrhizal fungi	Symbiont or beneficial organism	Present	(Dalpé 2003)
Nectria galligena (nectria canker) (= *Neonectria galligena*)	Pathogen	Present	(Farr and Rossman undated; Jones and Aldwinckle 1990)
Penicillium spp. (blue mold)	Pathogen	Present	(AAFC pathology database undated; Jones and Aldwinckle 1990)
Pezicula malicorticis (anthracnose perennial canker; bull's eye rot) (= *Neofabraea malicorticis*)	Pathogen	Present	(Farr and Rossman undated; Jones and Aldwinckle 1990)
Phytophthora spp. (phytophthora crown collar and root rot)	Pathogen	Present	(AAFC pathology database undated; Jones and Aldwinckle 1990)
Podosphaera leucotricha (powdery mildew)	Pathogen	Present	(Farr and Rossman undated; Jones and Aldwinckle 1990)

...mildew)			...Aldwinckle 1990)
Rhizopus stolonifer **(rhizopus rot)**	Pathogen	Present	(Farr and Rossman undated; Jones and Aldwinckle 1990)
Venturia inaequalis **(apple scab)**	Pathogen	Present	(Farr and Rossman undated; Jones and Aldwinckle 1990)

Table 4b: Examples of potential interactions of *Malus domestica* with Virus during its life cycle in a natural environment.

Other life forms	Interaction with *M. domestica* (pathogen; symbiont or beneficial organism; consumer; gene transfer)	Presence in Canada	Reference(s)
Apple chlorotic leafspot virus	Pathogen	Present	(AAFC pathology database undated; Jones and Aldwinckle 1990)
Apple mosaic virus	Pathogen	Present	(AAFC pathology database undated; Jones and Aldwinckle 1990)
Apple scar skin viroid (dapple apple viroid)	Pathogen	Present	(AAFC pathology database undated; Jones and Aldwinckle 1990)
Tomato ringspot virus	Pathogen	Present	(AAFC pathology database undated)

Table 4c: Examples of potential interactions of *Malus domestica* with Bacteria during its life cycle in a natural environment.

Other life forms	Interaction with *M. domestica* (pathogen; symbiont or beneficial organism; consumer; gene transfer)	Presence in Canada	Reference(s)
***Agrobacterium* spp. (crown gall, hairy root) (= *Rhizobium radiobacter; R. rhizogenes*)**	Pathogen	Present	(AAFC pathology database undated; Jones and Aldwinckle 1990)
***Erwinia amylovora* (fire blight)**	Pathogen	Present	(CABI 2012; Jones and Aldwinckle 1990)
***Pseudomonas syringae* pv. *papulans* (blister spot)**	Pathogen	Present	(CABI 2012; Jones and Aldwinckle 1990)

Soil microbes	Symbiont or beneficial organism	Present	

Table 4d: Examples of potential interactions of *Malus domestica* with Insects and Mites during its life cycle in a natural environment.

Other life forms	Interaction with *M. domestica* (pathogen; symbiont or beneficial organism; consumer; gene transfer)	Presence in Canada	Reference(s)
***Aculus schlechtendali* (apple rust mite)**	Consumer	Present	(CABI 2012))
***Ametastegia glabrata* (dock sawfly)**	Consumer	Present	(Smith 1979)
***Aphis pomi* (apple aphid)**	Consumer	Present	(CABI 2012)
***Apis mellifera* (European honeybee)**	Symbiont or beneficial organism	Present	(Free 1966)
***Archips* spp. (fruittree leafroller, European leafroller)**	Consumer	Present	(CABI 2012)
***Atractotomus mali* (apple brown bug)**	Consumer	Present	(AAFC 2011)
***Campylomma verbasci* (mullein bug)**	Consumer	Present	(Macnay and Creelman 1958; Thistlewood et al. 1990)
***Choristoneura rosaceana* (obliquebanded leafroller)**	Consumer	Present	(CABI 2012)
***Conotrachelus nenuphar* (plum curculio)**	Consumer	Present	(AAFC 2011)
***Cydia pomonella* (codling moth)**	Consumer	Present	(CABI 2012)
***Diaspidiotus* spp. (San Jose scale, European fruit scale)**	Consumer	Present	(Ben-Dov and German 2003)
***Dysaphis plantaginea* (rosy apple aphid)**	Consumer	Present	(CABI 2012)
***Epiphyas postvittana* (light brown apple moth)**	Consumer	Absent	(Brown et al. 2010)

moth)			
Eriosoma lanigerum (woolly apple aphid)	Consumer	Present	(CABI 2012)
Euschistus variolarius (onespotted stinkbug)	Consumer	Present	(Jamison 2005)
Frankliniella occidentalis (western flower thrips)	Consumer	Present	(CABI 2012)
Grapholita molesta (oriental fruit moth)	Consumer	Present	(AAFC 2011)
Halyomorpha halys Stal (brown marmorated stink bug)	Consumer	Present	(CABI 2012)
Hoplocampa testudinea Klug (European apple sawfly)	Consumer	Present	(AAFC 2011)
Hyphantria cunea (fall webworm)	Consumer	Present	(Drooz 1985)
Lepidosaphes ulmi (oystershell scale)	Consumer	Present	(Kosztarab 1996)
Lithophane georgii (green fruitworm)	Consumer	Present	(Troubridge and Lafontaine 2002; Troubridge and Lafontaine 2003)
Lygus lineolaris (tarnished plant bug)	Consumer	Present	(AAFC 2011)
Operophtera bruceata (Bruce spanworm)	Consumer	Present	(Drooz 1985)
Operophtera brumata (winter moth)	Consumer	Present	(AAFC 2011)
Orthosia hibisci (speckled green fruitworm)	Consumer	Present	(AAFC 2011)
Pandemis limitata (threelined leafroller)	Consumer	Present	(BCMA 2010)
Phenacoccus aceris (apple mealybug)	Consumer	Present	(Macnay and Creelman 1958)
Phyllonorycter blancardella	Consumer	Present	(CABI 2012)

Blancardella (tentiform leafminer)			
Rhagoletis pomonella (apple maggot)	Consumer	Present	(AAFC 2011)
Rhopalosiphum fitchii (apple grain aphid)	Consumer	Present	(Macnay and Creelman 1958)
Spilonota ocellana (eyespotted budmoth)	Consumer	Present	(CABI 2012)
Tetranychus spp. (McDaniel spider mite, twospotted spider mite)	Consumer	Present	(CABI 2012; Macnay and Creelman 1958))
Typhlocyba pomaria (white apple leafhopper)	Consumer	Present	(Macnay and Creelman 1958)

Table 4e: Examples of potential interactions of *Malus domestica* with Animals during its life cycle in a natural environment.

Other life forms	Interaction with *M. domestica* (pathogen; symbiont or beneficial organism; consumer; gene transfer)	Presence in Canada	Reference(s)
Animal browsers	Consumer	Present	(AAFC 2011)
Birds	Consumer	Present	(AAFC 2011)
Earthworms	Symbiont or beneficial organism	Present	Expert knowledge
Nematodes	Consumer; symbiont or beneficial organism	Present	(Jackson 2003)

Table 4f: Examples of potential interactions of *Malus domestica* with Plants during its life cycle in a natural environment.

Other life forms	Interaction with *M. domestica* (pathogen; symbiont or beneficial organism; consumer; gene transfer)	Presence in Canada	Reference(s)
Other *M. domestica*	Gene transfer	Present	(Kron et al. 2001)
Native crabapple (*M. fusca and M. coronaria*) and other introduced crabapple species and hybrids	Gene transfer	Present	(Kron and Husband 2007)

7. References

AAFC. 2011. Crop profile for apple in Canada, 2009. Pages 66. Pesticide Risk Reduction Program, Pest Management Centre, Agriculture and Agri-Food Canada (AAFC), Ottawa, ON.

AAFC. 2012. A snapshot of the Canadian apple industry, 2010. [Online] Available: www.agr.gc.ca/horticulture_e [2012].

AAFC pathology database. undated. Host-pathogen database (Beta/Demo-version 2012). Agriculture & Agri-food Canada (AAFC), Ottawa, ON.

Australian National Botanic Gardens. 2012. Australian plant name index (APNI). Integrated botanical information system (IBIS) database. [Online] Available: https://www.anbg.gov.au/apni/ [2012].

Bailey, L. G. and Bailey, E. Z. 1976. Hortus Third: A Concise Dictionary of Plants Cultivated in the United States and Canada. McMillan Publishing Co., New York, New York.

Banno, K., Hirano, Y., Ishikawa, H. and Kakegawa, M. 2003. Breeding and characteristics of symmetric intergeneric hybrids between apple and pear. Acta Horticulturae 622:265-276.

BCMA. 2006. Home garden factsheets - apples in your garden. [Online] Available: http://www.al.gov.bc.ca/treefrt/homegdn/apples.htm [2012].

BCMA. 2010. Tree fruit leafrollers. [Online] Available: http://www.al.gov.bc.ca/cropprot/tfipm/leafrollers.htm [2012].

BCMA. 2012. Apple scab management in British Columbia. [Online] Available: http://www.agf.gov.bc.ca/cropprot/tfipm/applescb.htm [2012].

Bell, R. L. and Leitão, J. M. 2011. *Cydonia*. Pages 1-16 *in* C. Kole, ed. Wild crop relatives: Genomic and breeding resources. Springer-Verlag, Berlin Heidelberg.

Belrose. 2012. World apple review. Belrose, Inc., Pullman, WA, USA.

Ben-Dov, Y. and German, V. 2003. A systematic catalogue of the Diaspididae (armoured scale insects) of the world, subfamilies Aspidiotinae, Comstockiellinae and Odonaspidinae. Intercept Ltd, Andover.

Boyer, J. and Liu, R. H. 2004. Apple phytochemicals and their health benefits. Nutrition Journal 3:5.

Brouillet, L., Coursol, F. and Favreau, M. 2010+. VASCAN, the database of vascular plants of Canada. [Online] Available: http://data.canadensys.net/vascan/ [2012].

Brown, J. W., Epstein, M. E., Gilligan, T. M., Passoa, S. C. and Powell, J. A. 2010. Biology, identification, and history of the light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae: Archipini) in California: an example of the importance of local faunal surveys to document the establishment of exotic insects. American Entomologist 56(1):34-43.

Brown, S. 2012. Apple. Pages 329-367 *in* M. L. Badenes, D. H. Byrne, eds. Fruit breeding. Springer Science + Business Media, LLC, New York, NY.

Brown, S. K. and Maloney, K. E. 2003. Genetic improvement of apple: Breeding, markers, mapping and biotechnology. Pages 31-59 *in* D. C. Ferree, I. J. Warrington, eds. Apples: Botany, production and uses. CABI Publishing, CAB International, Wallingford, UK.

CABI. 2012. Crop protection compendium. CAB International, Wallingford, UK.

CFIA and NRCan/CFS. 2011+. Plants of Canada Database. Canadian Food Inspection Agency and Canadian Forest Service. [Online] Available: http://www.plantsofcanada.info.gc.ca/ [2013].

Chagné, D., Carlisle, C., Blond, C., Volz, R., Whitworth, C., Oraguzie, N., Crowhurst, R., Allan, A., Espley, R., Hellens, R. and others. 2007. Mapping a candidate gene (MdMYB10) for red flesh and

foliage colour in apple. BMC Genomics 8(1):212.

Chagné, D., Crowhurst, R. N., Troggio, M., Davey, M. W., Gilmore, B., Lawley, C., Vanderzande, S., Hellens, R. P., Kumar, S., Cestaro, A. and others. 2012. Genome-wide SNP detection, validation, and development of an 8K SNP array for apple. PLoS ONE 7(2):e31745.

Coart, E., Van Glabeke, S., De Loose, M., Larsen, A. S. and Roldan-Ruiz, I. 2006. Chloroplast diversity in the genus *Malus*: new insights into the relationship between the European wild apple (*Malus sylvestris* (L. Mill.) and the domesticated apple (*Malus domestica* Borkh.). Molecular Ecology 15:2171-2182.

Coart, E., Vekemans, X., Smulders, M. J. M., Wagner, I., Van Huylenbroeck, J., Van Bockstaele, E. V. and Roldan-Ruiz, I. 2003. Genetic variation in the endangered wild apple (*Malus sylvestris* (L.) Mill.) in Belgium as revealed by amplified fragment length polymorphism and microsatellite markers. Molecular Ecology 12:845-857.

Crandall, C. S. 1926. Apple breeding at the Univ. of Illinois. Ill. Agr Expt Sta Bull 275.

Dalpé, Y. 2003. Mycorrhizal fungi biodiversity in Canadian soils. Canadian Journal of Soil Science 2003, 83 (Special Issue):321-330.

DeGrandi-Hoffman, G., Hoopingarner, R. and Klomparens, K. 1986. Influence of honey bee (Hymenoptera: Apidae) in-hive pollen transfer on cross-pollination and fruit set in apple. Environmental Entomology 15(3):723-725.

Dennis, F. 2003. Flowering, pollination and fruit set and development. Pages 153-166 *in* D. C. Ferree, I. J. Warrington, eds. Apples: Botany, production and uses. CABI Publishing, CAB International, Wallingford, UK.

Dickson, E. E., Kresovick, S. and Weeden, N. 1991. Isozymes in North American *Malus* (Rosaceae): Hybridization and species differentiation. Systematic Botany 162(2):363-375.

Drooz, A. T. 1985. Insects of eastern forests. USDA Forest Service miscellaneous publication No. 1426. Washington, D.C. 608 pp.

Duncan, W. H. and Duncan, M. B. 1988. Trees of the southeastern United States. University of Georgia Press, Athens, GA.

E-Flora BC. 2012. *Malus fusca*. Electronic atlas of the flora of British Columbia. [Online] Available: http://www.geog.ubc.ca/biodiversity/eflora/index.shtml [2012].

FAO. 2013. FAOSTAT. Food and Agriculture Organization of the United Nations Statistics Division. [Online] Available: http://www.fao.org/corp/statistics/en/ [2013].

Farr, D. F. and Rossman, A. Y. undated. Fungal databases, Systematic Mycology and Microbiology Laboratory, ARS, USDA. [Online] Available: http://nt.ars-grin.gov/fungaldatabases/ [2012].

Ferree, D. C. and Carlson, R. F. 1987. Apple rootstocks. Pages 107-143 *in* R. C. Rom, R. F. Carlson, eds. Rootstocks for fruit crops. John Wiley & Sons, New York, NY.

Flachowsky, H., Le Roux, P.-M., Peil, A., Patocchi, A., Richter, K. and Hanke, M.-V. 2011. Application of a high-speed breeding technology to apple (*Malus × domestica*) based on transgenic early flowering plants and marker-assisted selection. New Phytologist 192(2):364-377.

Flachowsky, H., Peil, A., Sopanen, T., Elo, A. and Hanke, V. 2007. Overexpression of BpMADS4 from silver birch (*Betula pendula* Roth.) induces early-flowering in apple (*Malus × domestica* Borkh.). Plant Breeding 126(2):137-145.

Flora of China editorial committee. 1959+. Flora of China. 80+ vols. [Online] Available: http://flora.huh.harvard.edu/china/mss/intindex.htm [2012].

Free, J. B. 1966. The foraging areas of honeybees in an orchard of standard apple trees. Journal of Applied Ecology 3(2):261-268.

Free, J. B. and Spencer-Booth, Y. 1964. The foraging behaviour of honey-bees in an orchard of dwarf apple trees. Journal of Horticultural Science 39(2):78-83.

Fruit breedomics consortium. 2012. [Online] Available: http://fruitbreedomics.com/ [2012].

Gessler, C. and Pertot, I. 2012. Vf scab resistance of *Malus*. Trees - Structure and Function 26(1):95-108.

Gleason, H. A. and Cronquist, A. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Second Edition. The New York Botanical Garden, Bronx, New York.

Hampson, C. R. and Kemp, H. 2003. Characteristics of important commercial apple cultivars. Pages 61-90 *in* D. C. Ferree, I. J. Warrington, eds. Apples: Botany, production and uses. CABI publishing, CAB international, Wallingford, UK.

Hancock, J. F., Luby, J. J., Brown, S. K. and Lobos, G. A. 2008. Apples. Pages 1-37 *in* J. F. Hancock, ed. Temperate Fruit Crop Breeding: Germplasm to Genomics. Springer Science+Business Media B.V., New York, NY.

Harris, S. A., Robinson, J. P. and Juniper, B. E. 2002. Genetic clues to the origin of the apple. Trends in Genetics 18(8):426-430.

Iezzoni, A., Weebadde, C., Luby, J. J., Chengyan, Y., van de Weg, E., Fazio, G., Main, D., Peace, C. P., Bassil, N. V. and McFerson, J. 2010. RosBREED: Enabling marker-assisted breeding in Rosaceae. Acta Horticulturae (ISHS) 859:289-294.

Ignatov, A. and Bodishevskaya, A. 2011. *Malus*. Pages 45-64 *in* C. Kole, ed. Wild crop relatives: Genomic and breeding resources Temperate fruits. Springer-Verlag, Berlin, Heidelberg.

Isaacson, R. T. and Allen, K. 2007. Plant Information Online. University of Minnesota Libraries. [Online] Available: www.plantinfo.umn.edu/ [2012].

Jackson, J. E. 2003. Biology of apples and pears. Cambridge University Press, Cambridge.

Jamison, T. 2005. Species page – *Euschistus variolarius*. Online database of the E.H. Strickland entomological museum, University of Alberta. [Online] Available: http://www.entomology.ualberta.ca/searching_species_details.php?s=5913# [2012].

Janick, J., Cummins, J. N., Brown, S. K. and Hemmat, M. 1996. Apples. Pages 1-77 *in* J. Janick, J. Moore, eds. Fruit Breeding, Volume 1: Tree and Tropical Fruits. John Wiley & Sons, Inc., Hoboken, NJ.

Jannink, J.-L., Lorenz, A. J. and Iwata, H. 2010. Genomic selection in plant breeding: from theory to practice. Briefings in Functional Genomics 9(2):166-177.

Jones, A. L. and Aldwinckle, H. S. 1990. Compendium of apple and pear diseases. American phytopathological society, St. Paul, Minnesota. vi + 100 pp.

Juniper, B. E., Watkins, R. and Harris, S. A. 1999. The origin of the apple. Proceedings of the Eucarpia symposium on fruit breeding and genetics 484:27-33.

Kartesz, J. T. 1999. Synthesis of the North American Flora Version 1.0 - A synonomized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. North Carolina Botanical Garden, Chapel Hill, NC.

Kartesz, J. T. 2011. North American Plant Atlas. [maps generated from Kartesz, J.T. 2010. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP). (in press)]. The Biota of North America Program (BONAP), Chapel Hill, NC.

Kemp, H. 1996. Pollination results of apple, *Malus*, pear, plum and cherry of the international working group on pollination. Pages 243-298 Acta Hort (ISHS)

Khan, M. A., Han, Y., Zhao, Y. F. and Korban, S. S. 2012. A high-throughput apple SNP genotyping platform using the GoldenGate™ assay. Gene 494(2):196-201.

Korban, S. S. 1986. Interspecific hybridization in *Malus*. HortScience 21(1):41-48.

Kosztarab, M. 1996. Scale Insects of northeastern North America. Virginia museum of natural history, Special publication number 3, Martinsville, VA. 650 pp.

Kotoda, N., Wada, M., Komori, S., Kidou, S., Abe, K., Masuda, T. and Soejima, J. 2000. Expression pattern of homologues of floral meristem identity genes LFY and AP1 during flower development in apple. Journal of the American Society for Horticultural Science 125(4):398-403.

Kron, P. and Husband, B. C. 2007. Assessing the risk of gene flow between cultivated apple (*Malus* x *domestica*) and its wild relative, *M. coronaria*: II Survival and fertility of hybrids. Report prepared for the Plant Biosafety Office, Canadian Food Inspection Agency. Pages 14. Department of Integrative Biology, University of Guelph, Guelph, ON.

Kron, P. and Husband, B. C. 2009. Hybridization and the reproductive pathways mediating gene flow between native *Malus coronaria* and domestic apple, *M. domestica*. Botany 87:864-874.

Kron, P., Husband, B. C., Kevan, P. G. and Belaoussoff, S. 2001. Factors affecting pollen dispersal in high-density apple orchards. HortScience 36(6):1039-1046.

Kumar, S., Bink, M., Volz, R., Bus, V. and Chagné, D. 2012a. Towards genomic selection in apple (*Malus × domestica* Borkh.) breeding programmes: Prospects, challenges and strategies. Tree Genetics & Genomes 8(1):1-14.

Kumar, S., Chagné, D., Bink, M. C. A. M., Volz, R. K., Whitworth, C. and Carlisle, C. 2012b. Genomic selection for fruit quality traits in apple (*Malus × domestica* Borkh.). PLoS ONE 7(5):e36674. doi: 10.1371/journal.pone.0036674.

Landcare Research. 1996-2012. Ngā Tipu o Aotearoa - New Zealand plants. [Online] Available: http://www.landcareresearch.co.nz/databases/db_details.asp?Database_Collection_ID=3 [2012].

Larsen, A. and Kjær, E. 2009. Pollen mediated gene flow in a native population of *Malus sylvestris* and its implications for contemporary gene conservation management. Conservation Genetics 10(6):1637-1646.

Larsen, A. S., Asmussen, C. B., Coart, E., Olrik, D. C. and Kjaer, E. D. 2006. Hybridization and genetic variation in Danish populations of European crab apple (*Malvus sylvestris*). Tree Genetics & Genomes 2:86-97.

Larsen, A. S., Jensen, M. and Kjær, E. D. 2008. Crossability between wild (*Malus sylvestris*) and cultivated (*M.* x *domestica*) apples. Silvae Genetica 57(3):127-130.

Laurens, F. 1999. Review of the current apple breeding programs in the world: objectives for scion cultivar improvement. Acta Horticulturae 484:163-170.

Little, E. L. J. 1979. Checklist of United States trees (native and naturalized). USDA agriculture handbook 541. USDA Forest Service, Washington, DC. 375 pp.

Luby, J. and Fennell, A. 2006. Fruit breeding for the Northern Great Plains at the University of Minnesota and South Dakota State University. HortScience 41(1):25-26.

Luby, J. J. 2003. Taxonomic classification and brief history. Pages 1-14 *in* D. C. Ferree, I. J. Warrington, eds. Apples: Botany, production and uses. CABI International, Cambridge, UK.

Mabberley, D. J., Jarvis, C. E. and Juniper, B. E. 2001. The name of the apple. Telopea 9(2):421-430.

Macnay, C. G. and Creelman, I. S. 1958. List of insects and mites affecting tree fruits in Canada. Canada Department of Agriculture, Science Service, Research Notes Series, Entomology, No. E-12. 38 pp.

Maggs, D., Martin, G. and Needs, R. 1971. The spread of cross-pollination in a solid block of Granny Smith apples. Australian Journal of Experimental Agriculture 11(48):113-117.

Myers, J. A., Vellend, M., Gardescu, S. and Marks, P. L. 2004. Seed dispersal by white-tailed deer: Implications for long-distance dispersal, invasion, and migration of plants in eastern North America. Oecologia 139:35-44.

Nova Scotia Department of Agriculture. 2009. Business planning and economics of apple orchard establishment and cost of production in Nova Scotia. [Online] Available: http://www.gov.ns.ca/agri/bde/news/pdfs/AppleProductionReport.pdf [2012].

O'Rourke, D. 2003. World production, trade consumption and economic outlook for apples. Pages 15-29 *in* D. C. Ferree, I. J. Warrington, eds. Apples: Botany, production and uses. CABI Publishing, CAB International, Wallingford, UK.

Orange Pippin Ltd. 2012. Orange Pippin fruit trees. [Online] Available: www.orangepippin.com [2012].

Palmer, J. W., Privé, J. P. and Tustin, D. S. 2003. Apple physiology and environmental influences - temperature. Pages 217-236 *in* D. C. Ferree, I. J. Warrington, eds. Apples: Botany, production and uses. CABI International, Cambridge, UK.

Papademetriou, M. K. and Herath, E. M., (eds.) 1999. Deciduous fruit production in Asia and the Pacific. Food and Agriculture Organization of the United Nations: Regional Office for Asia and the Pacific, Bangkok.

Parker, M. L. 1993. Apple rootstocks and tree spacing. Leaflet No. 300-A. [Online] Available: http://www.ces.ncsu.edu/depts/hort/hil/hil-300-a.html [September 2010].

Parker, M. L. and Unrath, C. R. 1998. High-density apple orchard management techniques. Leaflet no. HIL-360. [Online] Available: http://www.ces.ncsu.edu/depts/hort/hil/hil-360.html [September 2010].

Penn State University. 2013. Fruit production for the home gardener. [Online] Available: http://extension.psu.edu/plants/gardening/fphg [2013].

Potter, D., Eriksson, T., Evans, R. C., Oh, S., Smedmark, J. E. E., Morgan, D. R., Kerr, M., Robertson, K. R., Arsenault, M., Dickinson, T. A. and others. 2007. Phylogeny and classification of Rosaceae. Plant Systematics and Evolution 266:5-43.

Pratt, C. 1988. Apple flower and fruit: Morphology and anatomy. Horticultural Reviews 10:273-308.

Qian, G.-Z., Liu, L.-F., Hong, D.-Y. and Tang, G.-G. 2008. Taxonomic study of *Malus* section *Florentinae* (Rosaceae). Botanical Journal of the Linnean Society 158:223-227.

Qian, G.-Z., Liu, L.-F. and Tang, G.-G. 2010. Proposal to conserve the name *Malus domestica* against *M. pumila*, *M. communis*, *M. frutescens*, and *Pyrus dioica* (Rosaceae). Taxon 59(2):650-652.

Reim, S., Flachowsky, H., Michael, M. and Hanke, M.-V. 2006. Assessing gene flow in apple using a descendant of *Malus sieversii* var. *sieversii* f. *niedzwetzkyana* as an identifier for pollen dispersal. Environmental Biosafety Research 5:89-104.

Rieger, M. 2006. Introduction to fruit crops. Food Products Press, Binghamton.

Robertson, K. R., Phipps, J. B., Rohrer, J. R. and Smith, P. G. 1991. A synopsis of genera in

Maloideae (Rosaceae). Systematic Botany 16(2):376-394.

Robinson, J. P., Harris, S. A. and Juniper, B. E. 2001. Taxonomy of the genus *Malus* Mill. (Rosaceae) with emphasis on the cultivated apple, *Malus domestica* Borkh. Plant Systematics and Evolution 226:35-58.

Rom, R. C. and Carlson, R. F. 1987. Rootstocks for fruit crops. John Wiley & Sons, New York, NY. 494 pp.

Sanders, M. 1994. Steps to success in replanting. [Online] Available: http://www.agf.gov.bc.ca/treefrt/replant/Steps_to_Success_in_Replanting.pdf [September 2010].

Sassa, H., Mase, N., Hirano, H. and Ikehashi, H. 1994. Identification of self-incompatibility-related glycoprotiens in styles of apple (*Malus* x *domestica*). Theoretical and Applied Genetics 89:201-205.

Schuster, M. and Büttner, R. 1995. Chromosome numbers in the *Malus* wild species collection of the genebank Dresden-Pillnitz. Genetic Resources and Crop Evolution 42:353-361.

Scoggan, H. J. 1979. Flora of Canada. National Museums of Canada, Ottawa, Ontario.

Sedov, E. N. and Makarkina, M. A. 2008. Biochemical composition of fruit of apple cultivar clones and tetraploid forms. Russian Agricultura Sciences 34(2):71-73.

Shulaev, V., Korban, S. S., Sosinski, B., Abbott, A. G., Aldwinckle, H. S., Folta, K. M., Iezzoni, A., Main, D., Aru´s, P., Dandekar, A. M. and others. 2008. Multiple models for Rosaceae genomics. Plant Physiology 147:985–1003.

Smith, D. R. 1979. Nearctic sawflies IV. Allantinae: Adults and larvae (Hymenoptera: Tenthredinidae). Technical bulletin, science and education administration, United States Department of Agriculture. 172 [+24] pp.

Soejima, J. 2007. Estimation of gene flow via pollen spread for the orchard layout prior to the field release of apple transformants. Acta Horticulturae (ISHS) 738:341-345.

Solymar, B. 2004. Crop Profile for Apple in Canada. Pest Management Centre, Pesticide Risk Reduction Program, Agriculture and Agri-Food Canada, Ottawa, ON.

Stover, M. E. and Marks, P. L. 1998. Successional vegetation in cultivated and pasture land in Tomkins County, New York. J Torr Bot Soc 125:150-164.

Sudworth, G. B. 1967. Forest trees of the Pacific slope. Dover Publications. 455 pp.

Swanton, C. J. and Weise, S. F. 1991. Integrated weed management: the rationale and approach. Weed Technology 5:648-656.

Thistlewood, H. M. A., Borden, J. H. and McMullen, R. D. 1990. Seasonal abundance of the mullein bug, *Campylomma verbasci* (Meyer) (Heteroptera: Miridae), on apple and mullein in the Okanagan Valley. The Canadian Entomologist 122(11/12):1045-1058.

Troubridge, J. T. and Lafontaine, J. D. 2002. The moths of Canada. Part 1: Noctuoidea of western Canada. [Online] Available: http://www.cbif.gc.ca/prev/eng/species-bank/moths-of-canada/noctuoidea-of-western-canada/?id=1370403266394 [2012].

Troubridge, J. T. and Lafontaine, J. D. 2003. The moths of Canada. Part 2: Noctuoidea of eastern Canada. [Online] Available: http://www.cbif.gc.ca/spp_pages/noctuoidea/eastindex_e.php [2012].

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. and Webb, D. A. 1968. Flora Europaea. Volume 2 - Rosaceae to Umbelliferae. Cambridge University Press, Cambridge, UK.

Tyson, R. C., Wilson, J. B. and Lane, W. D. 2011. A mechanistic model to predict transgenic seed

contamination in bee-pollinated crops validated in an apple orchard. Ecological Modelling 222(13):2084-2092.

U.S. Apple Association. 2012. Industry statistics. [Online] Available: http://www.usapple.org/index.php?option=com_content&view=article&id=19&Itemid=17 [2012].

USDA-ARS. 2012. Germplasm Resources Information Network - (GRIN) [Online Database]. [Online] Available: http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl [2012].

USDA-NRCS. 2012. The PLANTS Database. [Online] Available: http://plants.usda.gov [2012].

van Dalfsen, K. B. 1989. Support systems for high-density orchards. British Columbia Ministry of Agriculture and Fisheries, Victoria, BC.

Vanblaere, T., Szankowski, I., Schaart, J., Schouten, H., Flachowsky, H., Broggini, G. A. L. and Gessler, C. 2011. The development of a cisgenic apple plant. Journal of Biotechnology 154(4):304-311.

Velasco, R., Zharkikh, A., Affourtit, J., Dhingra, A., Cestaro, A., Kalyanaraman, A., Fontana, P., Bhatnagar, S. K., Troggio, M., Pruss, D. and others. 2010. The genome of the domesticated apple (*Malus* x *domestica* Borkh.). Nature Genetics:833-839.

Vinson, J. A., Xuehui, S., Zubik, L. and Bose, P. 2001. Phenol antioxidant quantity and quality in foods: Fruits. Journal of Agricultural and Food Chemistry 49(11):5315-5321.

Way, R. D., Aldwinckle, H. S., Lamb, R. C., Rejman, A., Sansavini, S., Shen, T., Watkins, R., Westwood, M. N. and Yoshida, Y. 1990. Apples (*Malus*). Pages 1–62 *in* J. N. Moore, R. Ballington, eds. Genetic resources of temperate fruit and nut crops. International Society of Horticultural Science, Wageningen, Netherlands.

Webster, A. D. 2005a. The origin, distribution and genetic diversity of temperate tree fruits. Pages 1-11 *in* J. Tromp, A. D. Webster, S. J. Wertheim, eds. Fundamentals of Temperate Zone Tree Fruit Production Backhuys Publishers, Leiden, The Netherlands.

Webster, A. D. 2005b. Sites and soils for temperate tree-fruit production: Their selection and amelioration. Pages 12-25 *in* J. Tromp, A. D. Webster, S. J. Wertheim, eds. Fundamentals of temperate zone tree fruit production Backhuys Publishers, Leiden, The Netherlands.

Webster, A. D. and Wertheim, S. J. 2003. Apple rootstocks. Pages 91-124 *in* D. C. Ferree, I. J. Warrington, eds. Apples: Botany, production and uses. CABI Publishing, CAB International, Wallingford, UK.

Wertheim, S. J. 1991. *Malus* cv. Baskatong as an indicator of pollen spread in intensive apple orchards. Journal of Horticultural Science 66(5):635-642.

Westwood, M. N. 1993. Temperate-zone pomology: Physiology and culture. 3rd ed. Timber Press, Portland.

Williams, S. C. and Ward, J. S. undated. Scattering scats: White-tailed deer as seed dispersers. Available: http://www.ct.gov/caes/lib/caes/documents/plant_science_day/2007psd/williams2007.pdf [2010].

Willson, M. F. 1993. Mammals as seed-dispersal mutualists in North America. OIKOS 67(1):159-176.

Witmer, M. C. 1996. Annual diet of cedar waxwings based on U.S. biological survey records (1885-1950) compared to diet of American robins: Contrast in dietary patterns and natural history. The Auk 113(2):414-430.

Appendix 1: Species and hybrid species currently recognized in the genus *Malus*, according to the taxonomy database of the U.S. Department of

Agriculture Germplasm Resources Information Network GRIN) (USDA-ARS 2012)

Appendix 1
▶ Descriptive text:

	Latin name	Common name
1	*Malus ×adstringens* Zabel	
2	*Malus angustifolia* (Aiton) Michx.	Southern crab apple
3	*Malus ×arnoldiana* (Rehder) Sarg. ex Rehder	
4	*Malus ×asiatica* Nakai	
5	*Malus ×astracanica* hort. ex Dum. Cours.	
6	*Malus ×atrosanguinea* (hort. ex Spath) C. K. Schneid.	
7	*Malus baccata* (L.) Borkh.	Siberian crab apple
8	*Malus baoshanensis* G. T. Deng	
9	*Malus brevipes* (Rehder) Rehder	
10	*Malus chitralensis* Vassilcz.	
11	*Malus coronaria* (L.) Mill.	Sweet crab apple
12	*Malus crescimannoi* Raimondo	
13	*Malus ×dawsoniana* Rehder	
14	*Malus domestica* Borkh.	
15	*Malus doumeri* (Bois) A. Chev.	
16	*Malus florentina* (Zuccagni) C. K. Schneid.	Hawthorn-leaf crab apple
17	*Malus floribunda* Siebold ex Van Houtte	Japanese flowering crab apple
18	*Malus fusca* (Raf.) C. K. Schneid.	Oregon crab apple
19	*Malus halliana* Koehne	Hall crab apple
20	*Malus ×hartwigii* Koehne	
21	*Malus honanensis* Rehder	
22	*Malus hupehensis* (Pamp.) Rehder	Chinese crab apple
23	*Malus ioensis* (Alph. Wood) Britton	Prairie crab apple
24	*Malus kansuensis* (Batalin) C. K. Schneid.	

24	*Malus kansuensis* (Batalin) C. K. Schneid.	
25	*Malus komarovii* (Sarg.) Rehder	
26	*Malus leiocalyca* S. Z. Huang	
27	*Malus maerkangensis* M. H. Cheng et al.	
28	*Malus ×magdeburgensis* Hartwig	
29	*Malus mandshurica* (Maxim.) Kom. ex Skvortsov	Manchurian crab apple
30	*Malus ×micromalus* Makino	Kaido crab apple
31	*Malus ×moerlandsii* Door.	
32	*Malus muliensis* T. C. Ku	
33	*Malus ombrophila* Hand.-Mazz.	
34	*Malus orientalis* Uglitzk.	
35	*Malus orthocarpa* Lavallee ex anon.	
36	*Malus ×platycarpa* Rehder	Bigfruit crab apple
37	*Malus prattii* (Hemsl.) C. K. Schneid.	Pratt apple
38	*Malus prunifolia* (Willd.) Borkh.	Plumleaf crab apple
39	*Malus pumila* Mill.	Paradise apple
40	*Malus ×purpurea* (A. Barbier) Rehder	
41	*Malus ×robusta* (Carriere) Rehder	Siberian crab apple
42	*Malus sargentii* Rehder	Sargent's apple
43	*Malus ×scheideckeri* Spath ex Zabel	
44	*Malus sieversii* (Ledeb.) M. Roem.	
45	*Malus sikkimensis* (Wenz.) Koehne ex C. K. Schneid.	
46	*Malus ×soulardii* (L. H. Bailey) Britton	Soulard crab apple
47	*Malus spectabilis* (Aiton) Borkh.	Asiatic apple
48	*Malus spontanea* (Makino) Makino	
49	*Malus ×sublobata* (Dippel) Rehder	
50	*Malus sylvestris* (L.) Mill.	European crab apple
51	*Malus toringo* (Siebold) de Vriese	Toringo crab

51		
52	*Malus toringoides* (Rehder) Hughes	Cutleaf crab apple
53	*Malus transitoria* (Batalin) C. K. Schneid.	
54	*Malus trilobata* (Poir.) C. K. Schneid.	
55	*Malus tschonoskii* (Maxim.) C. K. Schneid.	Pillar apple
56	*Malus yunnanensis* (Franch.) C. K. Schneid.	
57	*Malus zhaojiaoensis* N. G. Jiang	
58	*Malus zumi* (Matsum.) Rehder	O-zumi