Genetics and Breeding of Pear

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Abstract

Although *Pyrus* consists of 22 primary species, nearly all scion breeding is focused on three species, including *Pyrus communis* (European pear), *Pyrus pyrifolia* (sand pear), *and Pyrus* × *bretschneideri* (white pear). Most scion breeding programs around the world are in one of two camps: those breeding for European (*P. communis*) soft- or firm-textured pears, and those breeding for crisp-textured Asian pears (*P. pyrifolia* and *P.* × *bretschneideri*). Intercrossing among species is typically limited, except in New Zealand where it is a core aspect of the breeding program. The lack of effective control of pests and diseases in pear combined with increased consumer preferences for fruits grown with low chemical inputs and low environmental impacts is driving breeding programs to incorporate plant resistance to major pests and diseases. On the other hand, the range of vigor-controlling rootstocks for pear production is limited. Quince (*Cydonia oblonga*) rootstocks are preferred in Europe, as they offer vigor control, precocity, and ease of propagation. To date, utilization of quince rootstocks in North America has been restricted due to their lack of cold tolerance. Identification and testing of cold hardy quince selections could change this. *Pyrus* rootstocks are currently preferred in North America and in Asia because of their cold hardiness; however, they are more vigorous than quince, yet their yield efficiency is lower. Thus, vigor control is among breeding targets for *Pyrus* rootstocks. Hybrids between *Pyrus* species are now being used to overcome some of these deficiencies and to include adaption to highly alkaline soils. In addition, other species, such as *Amelanchier*, are being tested for their potentials to confer dwarfing, excellent cold tolerance, potential non-host resistance to pear decline, resistance to fire blight, and good yield efficiency. Recent identification of genetic markers for scion vigor control and precocity is a positive step for future breeding of enhanced *Pyrus* rootstocks. Overall, the development of cultivars and rootstocks with new or improved characters would be facilitated by the availability of molecular markers for traits of interest. However, pear breeding programs lag behind those of apple in application of marker-assisted selection and genomic selection to speed-up cultivar/rootstock development, and to ensure programs are more effective and efficient in

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their utilization of available resources. As current genetic markers are validated in more populations, and the pear reference genome sequence undergoes further refinement, these technologies will play a larger role in pear breeding programs.

4.1 Introduction

Pear is assumed to be an ancient allopolyploid that behaves as a diploid ($2n = 2x = 34$) (Crane and Lewis 1940). There are three important centers of origin for the genus *Pyrus.* The first is in the mountainous regions of Western China, while the second is in Western Asia, comprising Afghanistan, India, Tajikistan, Uzbekistan, and western Tian-Shan, and the third is in the Caucasus Mountains. *Pyrus*, belonging to the family Rosaceae and subfamily Pomoideae, is a diverse genus that includes 22 primary species ranging from the mostly soft-textured European pear, *Pyrus communis* L., to the crisp-textured Asian sand pear, *Pyrus pyrifolia* (Burm.) Nak., and the Chinese white pear, *Pyrus* × *bretschneideri* Rehd. (Bell 1991).

In 2015, world production of pears has been estimated to be 26.6 million metric tonnes, with approximately 20 million metric tonnes of those being crisp-textured Asian-style pears (Belrose 2016). Breeding programs typically fall into one of two groups, those selecting new types of soft-textured European pears, mainly in Europe and North America, and those selecting crisp-textured pears, generally concentrated in South Korea, Japan, China, and New Zealand. Breeders of European pears tend to target such fruit characters, as harvest season extension, red skin color, good fruit size, flavor, improved textural attributes, storage ability, as well as growth habit, and resistance to various diseases and pests, especially against pear scab (*Venturia pirina* Aderh.), fire blight (*Erwinia amylovora* (Burrill) Winslow et al.), and pear psylla (Psyllidae: Psyllinae: *Cacopsylla* spp.) (Dondini and Sansavini 2012). In China, breeding program objectives include high fruit quality, early ripening, long shelf-life, large fruit size, resistance to both scab (*V. nashicola* Tanaka et Yamamoto) and black spot (*Alternaria alternata* (Fr.) Keissler pv. *kikuchiana*), and environmental adaptation through the use of a range of species, including *P.* × *bretschneideri, P. pyrifolia, P. ussuriensis* Maxim*., and P.* × *sinkiangensis* (Teng 2011). Furthermore, breeding programs in Japan focus on genetic improvement of *P. pyrifolia* cultivars, with breeding objectives targeting superior fruit quality, early ripening, self-compatibility, and multiple disease resistance for pear scab *(V. nashicola*) and black spot *(A. alternata*) (Saito 2016). As in Japan, Korean breeding programs focus predominantly on enhancement of *P. pyrifolia* cultivars. Breeding targets include season extension, storage ability, large fruit size, and high aroma, as well as pest and disease resistance, especially for leaf rot *(A. kikuchiana*) and pear scab (*V. nashicola*) (Shin et al. 2002); whereas, the New Zealand breeding program utilizes interspecific hybrids with major breeding objectives of producing convenient (not messy to eat) fruit with high levels of flavor that can be eaten either readily from the tree or after storage, but with a minimum storage life of three months. Furthermore, additional important breeding goals for the New Zealand program include increased fruit precocity and yield, high fruit quality free of internal disorders, variations in red skin colors, a range of fruit flavors and shapes, fruit skin that will not scuff, and disease resistance, especially to both fire blight and pear scab (*V. pirina*). The primary species used to generate interspecific pear hybrids in New Zealand include *P.* × *bretschneideri*, *P. pyrifolia,* and *P. communis*.

It is important to point out that the North American and European pear markets are dominated by a small number of old *P. communis* cultivars, such as 'Williams' Bon Chrétien,' also known as 'Bartlett', 'Conference', 'Abaté Fetel', and D'Anjou' that have been selected before 1900. Pear fruit consumption rates in these regions are generally either static or dropping (Belrose 2016). New cultivars have struggled to get a foothold in these markets. This may be

attributed, in part, to the dominance of a small number of supermarket chains, strong competition with other fruits in the marketplace, and changing Western consumer food demands (Brewer and Palmer 2011). Over the last few decades, consumers desire more convenient fruit and snack foods that are ready to eat, and with consistent quality. Developing products with these attributes would have a positive influence on the economic returns for producers (Brewer and Palmer 2011). Furthermore, new pear cultivars incorporating improved resistances, especially for pests and diseases that have the largest effects on profitable pear production, such as fire blight, pear psylla, and pear scab, are needed to achieve an additional goal of growing pears with low chemical inputs.

The minimal impact of new pear cultivars in European and North American markets contrasts with the situation in China, wherein traditional *P. ussuriensis* and *P.* × *bretschneideri* cultivars maturing in mid- to late-season (i.e., mid-August to September), such as 'Dangshan Suli', 'Yali', 'Nanguoli', and 'Xuehauli' comprise about 40% of all commercially grown cultivars (Cao et al. 2014). Over the past few decades, a substantial increase in Chinese pear production has been attributed, in part, to nearly 100 new cultivars, released to the pear industry over the last 50 years from government and university breeding programs (Belrose 2016). Several of these new cultivars, such as 'Cuiguan' mature very early to early (July to early August), thus extending the season for fresh-eating pear fruit.

Interestingly, despite decline in total pear production in Japan over the past 40 years by over 40%, there has been a reasonable uptake of new cultivars (≈14% in 2012) (Saito 2016). Old cultivars, such as 'Nijisseiki' and 'Chojuro' have been superseded by cultivars released from breeding programs, including 'Kosui' 'Hosui', and more recently 'Akizuki' and 'Nansui.' The success of these new cultivars has been attributed to traits, such as resistance to black spot and improved eating quality.

In comparison with other perennial fruit crops, traditional pear breeding is an expensive and lengthy process as seedling trees take longer to come into fruiting, and juvenile trees have many spines, rendering harvest and management difficult. Furthermore, interstocks are required when quince rootstocks are used for seedling growth, which adds time and expense to the process. Availability of adapted, compatible, and dwarfing precocious *Pyrus* rootstocks would be of great benefit to pear breeding programs and to the pear industry as a whole.

New genomic technologies would offer opportunities for accelerating development and increasing efficiency and effectiveness of breeding programs for developing new pear cultivars, as well as new and improved pear rootstocks.

This review focuses on modern pear breeding approaches, as well as genetics of key selection traits that are important for today's pear breeders. It summarizes recent genomic-related research aimed at improving efficiencies of pear breeding.

4.2 Breeding Systems

Pear has a gametophytic self-incompatibility (GSI) system that ensures pollen fertilization of ovules in flowers and subsequent seed production via outcrossing with other compatible pears. As many of the important horticultural traits in pear are likely controlled by multiple genes, this GSI system ensures that pear progenies are highly heterogeneous, with a wide diversity of possible phenotypes. Nevertheless, the three most important components of any pear breeding program are the following: (1) hybridization of parents, carrying traits of interest, to generate seedling populations expressing new and improved characters, (2) identification of desirable selections carrying those traits of interest among seedling populations, and (3) evaluation and testing of the best-performing selections.

4.2.1 Hybridization

4.2.1.1 Compatibility

GSI is a mechanism triggered by proteins coded by a single locus on linkage group (LG) 17 with multiple *S*-alleles that determine inhibition of

self-incompatible pollen tube growth without damaging self-compatible tubes (Dondini and Sansavini 2012). Genotypes possessing one *S*-allele in common are partially compatible, and under certain conditions may produce progeny that exhibit reduced fruit set and seed production, while those possessing the same two *S*-alleles are fully incompatible (Wang et al. 2017). To date, a large number of unique *S*-alleles have been identified, 28 in *P. communis* (Gharehaghaji et al. 2014; Goldway et al. 2009) and at least 48 across five Asian pear species (Wang et al. 2017). The repeated use of closely related parents in a breeding program may over time result in deleterious concentration of a few *S*-alleles in breeding material of potential value as parents. Of 133 *P. communis* cultivars assessed for their *S*-haplotypes, 75 are found to carry the *S101* allele, probably reflecting the extensive use of 'Bartlett' (*S101*/*S102*) as a parent (Goldway et al. 2009). An understanding of compatible and incompatible mating combinations is therefore critically important to a pear breeder, and this can be derived either from knowledge of the *S*-haplotype(s) of parent candidates, or through past knowledge of cross-performance.

There are no major incompatibility barriers to interspecific hybridization in *Pyrus,* and at least six naturally occurring hybrid taxa have been reported (Bell 1991). Zielinski and Thompson (1967) have found little evidence for hybrid sterility from interspecific hybridizations. However, post-zygotic gene flow barriers may exist between different *Pyrus* species. In New Zealand's pear breeding program, some progeny from crosses between Asian- and European pear-derived parents have shed either little or no pollen when anthers are dried (White and Brewer 2002). Hybrid necrosis (HN) of young pear seedlings has also been observed in some interspecific populations, but this has not been observed in intraspecific crosses. Two distinct HN phenotypic classes have been identified in a genomic mapping study of an interspecific ('PremP003' × 'Moonglow') pear population. These include the following: (i) seedlings that cease growing soon after germination, initially with chlorotic and necrotic leaf regions, then often dying within one month of germination ('Type 1'); and (ii) seedlings that initially develop normally, followed by termination of growth within three months after germination, with leaves beginning to cup downward and progressively becoming chlorotic and necrotic ('Type 2'). For those seedlings that grow normally, these have been classified as 'Type 3.' Interestingly, no significant differences in seed weight or radicle length among these 'Types' are observed in the above pear population at planting (Montanari et al. 2016a). Furthermore, 'Type 1': 'Type 2' + 'Type 3' ratios are consistent with a 3:13 segregation ratio, while Type 2:Type 3 ratios fit a 1:1 segregation ratio, thus indicating possible presence of major genes controlling this interspecific (sub)/lethality trait. In addition, at least a single two-gene epistatic interaction, between loci on LG1 and LG5, originating from Asian and European species, respectively, is attributed to incidence of Type 1 HN, with at least one other locus on LG2 implicated in regulating this phenotype. Molecular markers linked to both lethal phenotypes have been identified for these loci, and these will be useful in selecting parents lacking 'sublethal' alleles in order to maximize progeny numbers from interspecific crosses (Montanari et al. 2016a).

Self-compatibility

Incompatibility has been overcome following identification of a self-compatible natural mutant of 'Nijisseiki', referred to as 'Osanijisseiki' (Saito 2016). Crossing experiments have indicated that this self-compatibility is due to a mutation in the pistil *S* locus, resulting in deletion of the S-ribonuclease allele 4 (S4-RNase) in styles rather than in pollen. 'Osanijisseiki' has been used to develop a number of new self-compatible *P. pyrifolia* cultivars. In another approach, pollen from a heavily gamma-irradiated 'Kosui' tree has been used to pollinate 'Kosui' flowers. This has resulted in identifying a selection with a partial pollen mutation causing loss of pollen incompatibility function,

but retaining its stylar self-incompatibility (Sawamura et al. 2013; Saito 2016).

4.2.1.2 Pollen Collection and Storage

To ensure a full range of parents with different flowering times are available for intercrossing, pollen collection is best completed in advance of the crossing season (Bell et al. 1996). Pollen can be stored either from the previous year, or shoots of up to 1.2 m long, with their base cut along a 25° angle, can be collected at the tight-cluster flower stage before flowering begins, and kept in a greenhouse at 20–25 °C until flowers are fully open to collect anthers, and then extract pollen before dehiscence (van der Zwet et al. 1977). In addition, flowers at the balloon stage can also be collected from the orchard approximately 2 days before they are required (Visser and Oost 1981). Pollen can be extracted using a number of methods, including rubbing anthers over a wire mesh grid (1.5 mm^2) onto paper sheets (Bell et al. 1996), or combed from flowers using fine combs onto foil trays to maximize pollen recovery. Following extraction, pollen should be allowed to dry at approximately 23 °C for 24–48 h, either on a laboratory bench or in an incubator. While pear pollen remains viable at room temperature for 2–3 weeks, it is best refrigerated at approximately 3–5 °C in plastic or glass vials, and placed inside closed containers or stored in a desiccator with indicating silica gel over anhydrous $CaSO_4$ to remove moisture and maximize viability.

Pollen can be stored for 2 years at 2–4 °C and 10% relative humidity (Bell et al. 1996). Pollen can also be frozen at −20 to −120 °C for 2–3 years (Bhat et al. 2012). When pollen is required for use in the orchard, it is best that it is transported in a cooler bin or bag with frozen pads or similar receptacles to keep it chilled. Prior to use, pollen viability can be checked using acetocarmine or other stains following standard procedures (Bell et al. 1996). Pollen can also be germinated in a liquid medium containing 10% sucrose solution and 50 ppm boric acid, and germination rate recorded after 2 h at 23 °C (Visser and Oost 1981).

4.2.1.3 Emasculation, Pollination, and Seed Culture

Flowers are emasculated when the majority reaches balloon stage, at which point any open or excess flowers are removed. A variety of methods can be used for emasculation, including notched scissors, fine combs, finger nails, scalpels, or tweezers (van der Zwet et al. 1977; Bell and Janick 1990). Branches with emasculated flowers can be bagged or whole trees covered with insect proof nets and plastic tents to prevent insect visitation. However, many breeders do not think that this is necessary, as long as the calyx, corolla, and stamens are removed before flowers are open (Bell and Janick 1990). Pollination is ideally completed within 24–48 h following emasculation.

Although many cultivars have a stigma-receptive period of up to 6 to 11 days, some have a shorter receptive period that can cause a significant reduction in fruit set after 48 h from the start of anthesis; e.g., ‘Doyenné du Comice’ (‘Comice’) (Sanzol et al. 2003). In such cases, pollen can be applied to stigmas using a variety of tools, including the stopper of a pollen vial, glass rod, camel hair brush, strip cut eraser, and a fingertip (Bell et al. 1996; van der Zwet et al. 1977). In addition to the type of cultivar, temperature also strongly influences stigmatic receptivity, pollen tube growth, and/or ovule development for successful pollination. For example, ‘Comice’ has a shortened stigma receptivity period and reduced ovule longevity at 17 compared to 13 °C (Tromp and Borsboom 1994). Cool spring conditions decrease pollen tube growth, delay ovule degeneration, and can reduce the overall period for successful pollination (Sanzol et al. 2003).

Pear seeds extracted from fruit produced in crosses require a chilling period or stratification while in a moistened state to break dormancy and initiate germination (Bell et al. 1996). During stratification, seeds will absorb enough water to increase their weight by between 100 and 150% (Brewer, unpublished). Species originating from warm winter climates require a shorter stratification period, and the optimum temperature for

this process is higher (typically 7–10 °C) than for those from cold winter climates where the ideal stratification temperature is 3–5 °C for 60–90 days. Sowing media used by breeders to germinate seeds include a seedbed with a well-aerated medium, such as sand or vermiculite, finely ground peat moss (Bell et al. 1996), or dampened filter paper in petri plates or other closed containers (Montanari et al. 2016a). When grown on filter paper, any fungal development can be quickly identified and treated with a suitable fungicide before germinated seeds are planted (Montanari et al. 2016a). Once seeds have begun to germinate, warm periods of either one or more than 24 h at 20 °C can help stimulate consistent germination.

4.2.1.4 Seedling Growing Methods

Traditionally, pear seedlings grown on their own roots have long juvenility periods. In fact, generation cycles of up to 10 years have been reported for European pears (Brewer and Palmer 2011). Seedlings from Asian species are more precocious; i.e., they have significantly shorter generation cycles (Brewer et al. 2008a). Reduction of the generation cycle is a focus of many breeding programs, as this has the largest influence on the time taken for new products to reach the market (Brewer and Palmer 2011). Breeding systems have been developed to reduce the time taken for seedlings to come into bearing fruit. In New Zealand, seedlings are grown in the greenhouse to accelerate growth rate and increase internode numbers before planting them in an orchard or a nursery. In the orchard, tree top bending is applied when seedlings have produced at least 60 internodes. This bending has a number of benefits, such as reducing terminal growth while enhancing spur formation and flowering on mature wood. After bending the top of the tree, a full trunk girdle is completed, usually in the middle of summer (Brewer et al. 2008a). Fruit on seedling trees with bent tops are generally harvested from the ground, meaning ladders or other harvest devices are not required for the first 3 years of fruiting. Seedlings grown on their own roots are vigorous, and production of excess vegetative growth along with juvenile spines makes fruit thinning and harvest operations difficult. In New Zealand, seedlings are now managed by using rootstocks; wherein, seedlings are grown as fast as possible in a greenhouse (or temporarily in the orchard, if required) before budding or grafting onto elite Quince C rootstocks interstocked with elite 'Beurre Hardy.' The main benefit associated with utilizing rootstocks is improved ease of management, including crop regulation and harvest. Also, the outcome is more representative of what might be expected in commercial production of any future pear cultivar.

4.2.2 Polyploidy

Naturally occurring polyploidy has been identified in both European and Asian cultivars, including that of 'Sha 01', a tetraploid ($2n = 4x = 68$) bud mutant of 'Korla Pear' (Cao et al. 2002, 2014), a tetraploid 'Bartlett', and a triploid ($2n = 3x = 51$) 'Beurré Diel' (Moffett 1933), and 'Anli', a *P. ussuriensis* cultivar (Cao et al. 2002). Triploids have been developed by crossing naturally occurring or induced tetraploids (following colchicine treatment) with diploid parents. Even though there is a range of available polyploids, pear breeding programs rarely use these as to develop new cultivars. In crosses undertaken between Asian species, a range of tetraploid, triploid, and diploid combinations have been generated. For example, crosses between two tetraploids have yielded progeny of which 97% are tetraploid and 3% are aneuploid. Crosses of tetraploids with triploids, and reciprocal crosses, have yielded progenies with more or less equal numbers of triploids (34%), aneuploids (33%), and diploids (26%), while crosses between tetraploids and diploids have mostly produced diploids (61%) and triploids (36%) (Cao et al. 2002). Although there is little documented information on fruit traits in such polyploids, the wide range of phenotypic variations observed in leaf traits suggest there may be unexplored potential for variations in fruit traits among such polyploids (Sun et al. 2011).

4.2.3 Mutation Breeding

Mutagenic agents can be used to increase frequencies of mutations that would otherwise occur naturally at very low rates. Irradiation (X-rays) is the most common method used to modify well-adapted cultivars, typically to improve them for either one or two traits. However, many of these mutations are unstable, and only those that have proved to be stable have found a place in commercial production (Bell et al. 1996). The Food and Agriculture Organization of the United Nations (FAO)/International Atomic Energy Agency (IAED) Database (2000) records five European and two Japanese pear cultivars registered as new mutant cultivars (Ahloowalia et al. 2004). Most commercially available European pear cultivar mutations, whether naturally occurring or induced, involve enhancement of red fruit skin color. Such stable red skin color sports have been used in various pear breeding programs for developing new red-colored fruit skin cultivars.

Other mutations influencing disease resistance and responses to environment have been identified. For example, the most important mutations of Japanese pear include self-compatibility and resistance to black spot disease of 'Nijisseiki' and 'Shinsui'. These have now been used within the Japanese breeding program (Ahloowalia et al. 2004). Natural and induced mutations have also been identified for bloom time, blossom color, ripening period, and growth habit (Hancock and Lobos 2008).

4.3 Target Traits for Selection

A good knowledge of the genetics controlling a target trait of interest is critical in optimizing breeding strategies to maximize genetic gain and develop new cultivars carrying the desired trait. For those complex traits controlled by many genes, estimates of heritability and combining ability provide information of the relative importance of heredity compared with that of environment in determining an individual's phenotype. Narrow-sense heritability (h^2) estimates the extent to which a phenotype is determined by parental genes that are largely additive in their effects. While general combining ability (GCA) measures the average performance of a parent based on the performance of its progeny, specific combining ability (SCA) measures the additional genetic value due to interactions between particular parent genotypes.

In this section, key desirable traits targeted for selection in pear programs will be discussed in detail, including how the trait is measured and what is currently known regarding its genetics.

4.3.1 Fruit Quality

Improved fruit quality is the cornerstone of every pear breeding program. Fruit quality is a complex trait, being a culmination of all external and internal characters of the fruit deemed of commercial importance. Contributing characters to fruit quality include the following: texture; flavor; sweetness; sourness; skin scuffing; skin russet; physiological disorders; levels of bitterness; astringency; absence of grit cells within flesh, skin, and around core tissues; skin color; general appearance; post-harvest performance; and shelf-life. Breeders in different geographic regions place different emphasis on each of these traits in selecting cultivars that perform best for their specific breeding objectives under their climatic conditions.

Breeders often rate overall fruit quality using a composite score, determined from an amalgamation of phenotypic scores of many of the individual traits listed above. This is predominantly a hedonic score, and thus its narrow-sense heritability is often very low (Bell et al. 1996). It has been suggested that eating quality in European pear is governed by non-additive gene effects (i.e., through dominance and/or epistasis), while narrow-sense heritability is completely absent for this trait (Bell et al. 1996). Furthermore, specific combining ability (SCA) is much more important, thus suggesting that effective genetic gain for eating quality could be made by selecting for individuals within families with high SCA (Bell et al. 1996). In other studies,

heritability for overall fruit quality of either European pear or for mixed European and Asian pear families is low (h^2 = 0.09–0.1) (White et al. 2000b). The heritability of a selection index for overall fruit quality weighted each trait in terms of importance before summing individual scores is also low (h^2 = 0.17) (Bell and Janick 1990).

Environmental factors and developmental (maturation and ripening) stages can have considerable influences on many aspects of pear fruit quality (Bell and Janick 1990). Although their interactions with genotypes have not been formally documented, they must either be controlled or accounted for in order to accurately estimate genetic effects on fruit quality within a pear population. Pears of Asian parentages can be harvested either near or at full eating ripeness when fruit starch has been converted into sugar. In fact, tasting of the fruit may help determine stage of maturity. For those genotypes wherein skin color changes during maturation, background color changes from green to yellowish-green which can signal optimum maturity. Changes in flesh firmness (as measured hedonically or with a penetrometer) can also be a useful measure of maturity. Furthermore, likely commercial handling of fruit should also be taken into consideration; i.e., fruit harvested at an earlier stage of maturation for storage versus fruit that will be consumed immediately after picking.

In contrast to Asian pears, fruit of most European pears usually requires storage at cold temperatures to induce proper ripening (Sugar et al. 2009). Lengths of chill induction periods required for European pear vary among different cultivars. Summer maturing pears require a much shorter induction or no induction period (Bower et al. 2003) compared with later maturing pears, such as 'Comice' and 'Beurré D'Anjou' ('Anjou'), which require 4 and 6 weeks of cold storage, respectively; however, this is also dependent upon harvest time (Sugar et al. 2009). If fruits are left on trees to ripen, internal browning and other physiological disorders can often develop during storage or during shelf-life. Therefore, fruits are harvested well before ripening when skin background color is still green, and the flesh is hard and dry. For these fruit types, firmness and initiation of starch hydrolysis (using a starch pattern index) may serve as useful indicators to determine optimum harvest time. Ideally, several samples should be harvested from each seedling as fruit matures to ensure that fruit from at least one of these fruit samples has been collected at optimum harvest time.

4.3.1.1 Texture

Texture is a term used for the overall feel of food in the mouth and comprises properties that can be evaluated by touch. It can include biochemical components, such as particle size and shape, moisture content, lipid content, and cell wall composition, as well as mechanical factors (Sams 1999). Breeding programs often measure pear texture using a hedonic scale, which summarizes influences of fruit firmness, hardness, juiciness, flesh coarseness, grittiness, chewiness, crispness, fruit fiber, skin chewiness, and oral sensory response. This collective 'eating experience' has a very important influence on consumer acceptability of new products (Sams 1999). Although the genetics of pear texture is still poorly understood, seedling populations tend to reveal continuous segregation for this trait, with a general likelihood for polygenic control (Bell and Janick 1990). Bell (1991) has suggested that moderate genetic gain could be achieved through mass selection for texture as relatively large ratios of GCA to SCA variance along with moderate narrow-sense heritability (h^2 = 0.30) have been observed.

Firmness of ripe pear fruit varies considerably among species. European pears are generally eaten when soft, whereas Asian pear types are eaten firm. Most breeding programs concentrate on one or the other, thereby attending to local consumer demand for pear fruit that they are accustomed to.

In most European pear breeding programs, soft, melting, or buttery, and juicy textures are most commonly selected for (Bell et al. 1996), although occasionally either firm (Batlle et al. 2008) or 'almost' crisp textures, similar to 'Abaté Fétel', are also selected. In a study involving 10 European pear seedling populations, wherein

fruit are stored for 70 days at 0.5 °C followed by 7 days at 20 °C, White et al. (2000a, b) have found firmness heritability to be low (h_2 = 0.06). This may reflect the low genetic variation observed for fruit firmness among parents used in the study, and that ripening–inducing conditions have been adequate for this population.

In contrast, heritability for fruit firmness estimated for either Asian or interspecific hybrid pear seedling populations tends to be moderate to high. For example, heritability estimates have ranged from 0.14 to 0.56 for *P. pyrifolia* in a Japanese breeding program (Saito 2016; Abe et al. 1995), while estimates of 0.70 have been reported in *P. pyrifolia*, *P. ussuriensis,* and *P.* × *bretschneideri* seedling populations in a Korean breeding program (Shin et al. 2008). In New Zealand, heritability estimates for seedling populations with Asian, European, and interspecific hybrid parentages (White et al. 2000b) or of pear germplasm, including accessions of the same pear species, as well as those of interspecific hybrids, are high (h^2 = 0.62–0.67) (Kumar et al. 2017). Good genetic progress can be expected to be made in breeding for firm (or soft) textures from such seedling populations where a wide range of fruit firmness is present.

Juiciness is an important component of fruit quality in both European and Asian pears. In European pear, this trait is under both polygenic and monogenic controls (Hancock and Lobos 2008; Zielinski et al. 1965). Using a hedonic method of evaluation for juiciness along a 0–9 scale, White et al. (2000b) have reported that there is a low heritability for juiciness (h^2 = 0.04) in European seedling populations, thereby indicating there is little variation present in parents used. Moreover, when Asian and interspecific seedling populations are incorporated in the analysis, a slightly higher value (h^2 = 0.21) is observed.

Finally, for breeding programs of both European and Asian pears, there is strong selection against presence of grit or stone cells in flesh (h^2 = 0.57), skin, and to a lesser extent around the core, as well as toward fine (rather than coarse) texture (Bell and Janick 1990).

4.3.1.2 Flesh Color

Although white and cream are the most common flesh colors present in pear, green, yellow, pink, and red colors are also known to naturally occur. Segregation for white- and green-colored fruit flesh is controlled by a single gene, with white color being dominant, while green or cream colors serving as alternative alleles (Bell et al. 1996). Furthermore, segregation of progeny from crosses between the red-fleshed 'Sanquinole' and the white-fleshed 'Conference' has revealed that red flesh is dominant over white flesh (Bell et al. 1996).

4.3.1.3 Flavor

Flavor is an important attribute of any pear cultivar. It encompasses a combination of sweetness, sourness, bitterness, and astringency of oral sensory characters of pear fruits, along with volatile components sensed in the nose and throat (Brewer et al. 2008b; Dondini and Sansavini 2012; Bell et al. 1996). An important aspect of flavor is the sugar–acid balance, which is enhanced by the presence of volatiles, particularly in European pears (Eccher Zerbini 2002). As the presence of volatiles in Asian pear is less important, breeders have placed greater emphasis on high sugar levels when selecting genotypes for commercialization. Heritability estimates for overall flavor, from subjective scores, vary from low (h^2 = 0.06) in *P. communis* seedling populations to high (h^2 = 0.54) in interspecific hybrid seedling populations (Bell and Janick 1990).

4.3.1.4 Fruit Sweetness

High fruit sweetness is important for market acceptance of any pear cultivar (Jaeger et al. 2003). Sweetness, scored subjectively on a hedonic scale or assessed as soluble solids concentration, is a quantitative trait (Hancock and Lobos 2008). In an early study by White et al. (2000b), heritability of sweetness in European pear seedling populations and in hybrid European–Asian pear seedling populations is found to be low, h^2 = 0.05 and h^2 = 0.07, respectively, and similar to that (h^2 = 0.05) reported by Shin et al. (1983). These seedling populations have

been developed from crosses among parents selected for 'ideal' levels of sugar.

In contrast, Abe et al. (1995) have reported much higher heritability values (h^2 = 0.37–0.5) using randomly selected combinations of hybrid seedlings from the Japanese pear breeding program at the National Agriculture and Food Research Organization (NIFTS). Progress in breeding for higher sweetness in pear fruit could be achieved by selecting for genotypes with high flesh fructose concentrations. On a mole-to-mole basis, fructose has a perceived sweetness that is ~1.4–2-fold higher than other storage sugars present in pear fruit, including sucrose, sorbitol, and glucose (Harker et al. 2002; Saito 2016). Storage sugars in pear fruit consist of fructose, glucose, sorbitol, and sucrose (Saito 2016; Viera et al. 2013). In a New Zealand study on seedling populations of interspecific hybrids with different proportions of European, Japanese, and Chinese (*P.* × *bretschneideri*) parentages, average sugar levels are found to consist of 59% fructose, 13% glucose, 20% sorbitol, and 8% sucrose (Viera et al. 2013). In a Japanese study including 79 Asian cultivars from Japan, Korea, and China, it is reported that average percentage concentrations of these sugars are found to consist of 36.7% fructose, 15.2% glucose, 23.8% sorbitol, and 24.4% sucrose. In the New Zealand study, individual sugar levels of glucose, fructose, and sucrose contributed to higher genetic variance relative to total phenotypic variance (0.54–0.86) compared with that for total sugars (0.31). Interestingly, sorbitol levels have negative genetic correlation (rG = −0.65) with fructose, a relationship that warrants further investigation. Thus far, genetic markers associated with soluble solids concentration have been identified on LG10, LG5, and LG14, in an F1 population of 'Bayuehong' × 'Dangshansuli', but these have not been detected in all tested years (Wu et al. 2014).

4.3.1.5 Fruit Acidity

Organic acids are yet another significant component of pear fruit flavor serving to balance sweetness. For European pears, a range of acidity between pH 2.4 and 5.4 can be acceptable in commercial cultivars (Bell et al. 1996; Hancock and Lobos 2008). Levels of total organic acid vary within *Pyrus* taxa, wherein an average of 5.98 mg g^{-1} total organic acids has been reported for *P. ussuriensis*, 3.07 mg g^{-1} for *P.* × *bretschneideri*, 2.66 mg g^{-1} for *P. pyrifolia*, and 2.42 mg g^{-1} for *P. communis* (Sha et al. 2011). Moreover, relative and absolute acid levels can also be influenced by the environment (Hudina and Štampar 2004; Sha 2012; Sha et al. 2011). Thus, levels of individual organic acids present in both European and Asian pears can also vary. While malic and citric acids typically dominate, quinic, oxalic, shikimic, fumaric, tartaric, succinic, acetic, and lactic acids are also present (Liu et al. 2016; Sha et al. 2011). Fruit of *P. communis* is found to have higher acetic acid levels, while fruit of *P. ussuriensis* has higher quinic acid levels than those of other *Pyrus* species (Sha et al. 2011). Furthermore, malic and citric acids exhibit significant positive phenotypic correlations with quinic acid; whereas, significant negative correlations are observed between acetic and lactic acid and between quinic and tartaric acids (Sha et al. 2011).

In New Zealand, heritability of acidity evaluated on a hedonic scale was low in both European seedling populations alone, and when Asian and interspecific seedling populations were included, h^2 = 0.07 and 0.09, respectively (White et al. 2000b). Low heritability (h^2 = 0.17) for titratable acid was also identified through a genome-wide association study (GWAS) that included European, Asian, and interspecific hybrids (Kumar et al. 2017). However, Liu et al. (2016) reported high heritability of individual acids, including oxalic (h^2 = 0.88, 0.57), quinic (h^2 = 0.71, 0.58), malic (h^2 = 0.83, 0.77), shikimic (h^2 = 0.82, 0.50), and citric (h^2 = 0.75–0.80), when these were measured in consecutive years in progeny of a reciprocal cross of 'Dangshansuli' × 'Hosui.' It has been suggested that there was a maternal influence for inheritance of these acids. Thus, when breeding for lower acid levels, a parent with the lowest levels of oxalic, quinic, malic, and shikimic acids should be used as the female parent.

Single-nucleotide polymorphisms (SNPs) linked to titratable acidity have been identified on LG2 in a biparental cross between European and Asian species, and also in a genotyping-by-sequencing (GBS) study including European, Asian, and interspecific hybrids (Liu et al. 2011). A SNP associated with titratable acidity was also identified on LG7 in a New Zealand GBS study (Kumar et al. 2017).

4.3.1.6 Fruit Volatiles

Aromatic volatiles complement the sugar/acid balance in fruit and provide a cultivar's distinctive flavor. This is important for European pear cultivars, as they have a wide range of flavors, from the subtle 'Comice' (Eccher Zerbini 2002) to the strong distinctive flavor of 'Bartlett'. A total of 77 volatile compounds have been identified in fruit of 'Bartlett' (Bell et al. 1996), with decadienoate esters contributing the most to its characteristic flavor (Eccher Zerbini 2002). Fruits of other cultivars and selections, developed in breeding programs, with high levels of decadienoate esters are also deemed to possess a 'Bartlett' flavor.

Fruits of Asian pear cultivars are not typically known for their strong aromas, particularly those of Japanese pear, *P. pyrifolia*. However, fruits of some cultivars of *P. ussuriensis* have strong aromas, and these differ in their volatile compound compositions from those found in *P. communis* (Kang 2010). In addition, fruits of *P. ussuriensis* cultivars exhibit a very wide range of olefins, esters, alkanes, aldehydes, phenols, and ketones, and these cultivars serve as valuable breeding material for these aromatic compounds. Li et al. (2004) have identified variations in complex levels of volatile compounds in fruits of cultivars of *P. ussuriensis*, *P. communis*, *P.* × *bretschneideri,* and *P. pyrifolia*. Therefore, it is suggested that inheritance of these compounds is quantitative, and controlled by multiple genes. Analysis of 16 different volatile compounds from two families of *P.* × *bretschneideri* × *P. ussuriensis* has demonstrated high heritabilities for acetone, ethanol, propyl alcohol, and aldehyde, moderate heritabilities for ethylene, isopropanol, propionate ethyl, isovalerate, and low heritabilities for isopentanol and hexanol acetone (Li et al. 2004).

Breeding for flavors complemented by aromatic compounds is an important objective for the New Zealand Institute for Plant and Food Research Ltd (PFR) pear breeding program. Crosses among *P. communis*, *P. pyrifolia,* and *P.* × *bretschneideri* have generated interspecific hybrids bearing fruit with a wide range of different flavors (Brewer et al. 2008b). Adverse flavors, such as alcoholic, grassy, and high acid, are selected against. Interestingly, it has also been possible to select for pears with novel flavors that can develop when fruit are either on the tree and/or at any time during storage. Some individual selections bear fruit that do not seem to produce perceivable volatile flavors (Brewer et al. 2008b), while others bear fruit requiring chill induction before volatile flavors develop. Clearly, there is much for pear breeders to learn in developing cultivars carrying fruit with specific flavors (Xue et al. 2017b).

It is important to point out that those favorable flavors detected in fruit flesh are rarely identified in the skin. This may indicate that flavor development is differentially regulated in these tissues. Although bitterness, grassiness, and astringency can often be present in fruit skin, these are not perceived in fruit flesh (Brewer et al. 2008b).

4.3.1.7 Astringency and Bitterness

While all breeding programs for fresh consumption pears actively select against astringency and bitterness in fruit flesh, often little attention is paid to fruit skin or areas around the core. Breeding for cultivars destined for perry production is an exception, where both bitterness and astringency are desired (Bell et al. 1996). Low levels of astringency and bitterness can be acceptable for fresh consumption when this enhances the overall flavor perception. Bitterness and astringency are associated with presence of phenolic and polyphenolic compounds, including tannins and leucoanthocyanins (Bell et al. 1996). High levels of fruit astringency can be present when wild germplasm is used as parents in crosses for introgression of other desirable traits. In the New Zealand PFR breeding program,

bitterness is often detected in the skin of fruit of seedlings, but not as much in flesh of this fruit. Population-level improvements in decreasing bitterness and astringency have been reported, as both traits have virtually disappeared by the third generation (Brewer et al. 2008b), even though early research has indicated that there is a low heritability ($h^2 = 0.01$) for astringency (White et al. 2000b).

4.3.1.8 Fruit Size

Fruits of various pear species exhibit wide ranges for fruit size, as this is influenced by genetics, environment, and management factors, such as water availability, fruit set, fruit thinning, and overall crop load. *P. calleryana* and *P. betulaefolia*, commonly used as rootstocks, can bear fruit as small as 1 cm in diameter (Hancock and Lobos 2008). These species would require several generations of improvement for fruit to reach a suitable commercial size and eating quality. Cultivars of European, Japanese, and Chinese white pear, such as 'Uvedales Saint Germaine', 'Dongguanli', and 'Xuehuali', respectively, can produce very large fruit (Cao 2014). Pear fruit size is under polygenic control, but a range of heritability values, depending on the population used (Hancock and Lobos 2008). For example, in the NIFTS program in Japan, heritability values of $h^2 = 0.57–0.82$ have been reported for *P. pyrifolia* (Saito 2016), and in the Korean breeding program, heritability values ranging between $h^2 = 0.09$ and $h^2 = 0.85$ have been reported for interspecific hybrid populations among *P. pyrifolia*, *P. ussuriensis,* and *P.* × *bretschneideri* (Shin et al. 2008). In this latter study, heritability variations are dependent on the parental cultivar used in these crosses. For example, 'Whangkeumbae' and 'Gamcheonbae' are found to have high heritabilities, $h^2 = 0.76–0.85$ and $h^2 = 0.47–0.84$, respectively, for fruit size, while 'Niitaka' has a low heritability ($h^2 = 0.11–0.29$).

Quantitative trait loci (QTL) were identified for fruit weight in progeny of 'Bayuehong' × 'Dangshansuli' population, with a marker located at 16.3 cM from a QTL identified on LG17 of 'Dangshansuli'. In the second year of this study, marker Pyb13_250, associated with fruit size, was identified at 99.3 cM on LG13 of 'Bayuehong.' Additional research should be conducted to validate these markers.

4.3.1.9 Functional Compounds

To date, breeding programs have put very little effort into improving health attributes of pear fruit by increasing levels of bioactive compounds. However, consumer preferences are increasingly focused on health-promoting qualities of fruits and vegetables, and consumers can make purchasing decisions based on phytonutrient levels present in these foods (Patil et al. 2016). Researchers have quantified some bioactive compounds present in pear cultivars and germplasm (Abaci et al. 2016; Kolniak-Ostek 2016; Galvis Sánchez et al. 2003; Tanrıöven and Ekşi 2005; Yim and Nam 2015). Fortunately, presence of significant differences in contents of these bioactive compounds among pear cultivars offers opportunities for improvement in future breeding efforts, as does higher concentrations of anthocyanins in red skin and flesh of pear (Abaci et al. 2016; Yim and Nam 2015). Promotion of cultivars with research-supported health benefits is already underway (Sarkar et al. 2015; Stephenson 2015; Barbosa et al. 2013).

4.3.1.10 Storage Period and Shelf-life

Maintaining fruit in good condition during cool storage and until the point of sale is an important attribute of any new cultivar, and it is an important goal in many breeding programs (Bell et al. 1996). The PFR interspecific pear breeding program selection is strongly directed toward fruit that retains high-quality texture attributes following a minimum cold storage period of two months at 0.5–3 °C (Brewer et al. 2008b). Results from segregating seedling populations indicate that fruit storage potential is under polygenic control (Bell et al. 1996). Thus, there are several reasons why fruit may fail storage testing. The most common of these are

post-harvest disorders, such as internal browning, chilling injuries, and flesh spot decay (Brewer et al. 2008b).

Fruit ethylene production at harvest has been negatively associated with storage life in *P. pyrifolia*. Ethylene production in pear is controlled by two *1-amino-cyclopropane-1-carboxylic acid* (*ACC*) synthase genes, *pPPACS1* and *pPPACS2*, with dominant alleles associated with high and moderate ethylene levels, respectively. *PPACS2* has been mapped along the top of LG15 in *P. pyrifolia* (Itai et al. 1999). Many older Japanese pear cultivars carry the dominant *pPPACS1* allele, while newer cultivars tend to possess both recessive alleles. This finding reflects selection for material with longer storage/shelf-life and lower ethylene production in modern Japanese pear breeding programs (Itai and Fujita 2008). Restriction fragment length polymorphism (RFLP) markers for these two genes have been developed to predict low ethylene production in pear material in breeding programs (Itai and Fujita 2008). Interestingly, regulation of genes controlling ethylene production in *P.* × *bretschneideri* cultivars that are either climacteric ('Yali') or non-climacteric '(Hongli') is suggested to be similar to that observed in *P. pyrifolia* (Yamane et al. 2007). However, *P. communis* cultivars do not carry these *pPPACS* haplotypes (Oraguzie et al. 2010), thus suggesting presence of a separate system of ethylene control.

A long shelf-life for fruit following cold storage is also important for any newly released cultivar. Therefore, many breeding programs target a set shelf-life period following cold storage. At PFR, a period of seven days at 20 °C is a minimum standard used to simulate a typical time period for purchase and consumption of fruit (Brewer et al. 2008b). Taking advantage of the extended shelf-life inherent in many old Chinese pear cultivars, the New Zealand program maintains fruit from the best seedlings on a shelf at 20 °C until they either rot, turn internally brown, or shrivel. This approach has allowed for identification of advanced selections for up to 30 days of shelf-life following cold storage (Brewer and Palmer 2011).

4.3.2 Fruit Attractiveness

4.3.2.1 Fruit Shape

Pear fruit shape is under polygenic control with round and ovate shapes observed more frequently than pyriform and turbinate shapes in Asian, European, and interspecific hybrid seedling populations (White and Alspach 1996). A high heritability ($h^2 = 0.55$) for fruit length:-maximum width ratio suggests a relatively rapid progress can be made in breeding for fruit shape (White et al. 2000a). For European pear, acceptable genetic advances could be made for pyriform curvature ($h^2 \sim 0.5$), whereas the location of the point of maximum curvature has a low heritability ($h^2 = 0.01$) (White et al. 2000a). Therefore, identification of fruit shapes that are different from the typical pyriform fruit can be made, especially when pyriform-fruited parents are crossed with parents with either round- or ovate-shaped fruit.

4.3.3 Fruit Skin Ground Color

Background color of pear fruit skin is dependent on the relative concentrations of green (chlorophyll) and yellow (carotenoid) pigments present in the skin epidermis. During the ripening process in most pear cultivars, background color changes from green to either yellow-green or yellow following increase of carotenoids and/or breakdown of chlorophyll; however, the timing of this color change can vary considerably (Bell et al. 1996). In some cultivars, such as 'Conference' the skin remains fully green, but only turns yellow when the fruit is fully ripe, while for other cultivars, this change occurs at the onset of ripening; e.g., 'Packham's Triumph'. Genetic studies in European pear indicate that background skin color is controlled by a major gene, with yellow being dominant over green (Hancock and Lobos 2008). Inoue et al. (2006) have used a bulk segregant analysis of two F1 Japanese pear progenies to identify a 425-bp random amplification of polymorphic DNA (RAPD) marker associated with green skin color exhibiting a recombination rate of 7.3%. This RAPD

marker has been converted into a RAPD sequence-tagged site (STS) marker to identify a QTL at the top of LG8 at 2.2 cM (Yamamoto et al. 2014; Inoue et al. 2006).

4.3.4 Fruit Skin Over-Color

Red fruit over-color is an important breeding target for many programs around the world, as it can greatly enhance attractiveness of fruit (Brewer and Palmer 2011). Currently, red-skinned pears are sold at higher prices in international markets (Steyn et al. 2005). This is due to the low volume of these cultivars, but they also have high eating and storage qualities. Red color pigmentation is the result of accumulation of anthocyanins, specifically of cyanidin3-glactoside and cyanidin3-arabinoside, which are secondary metabolites synthesized, via the flavonoid biosynthetic pathway, in hyperdermal layers of the skin (Steyn et al. 2005; Thomson et al. 2018). Genetic expression of these anthocyanins is highly heritable, and hence can be readily exploited in breeding programs. However, anthocyanin levels are not always consistent, as these can change during fruit development, and may also vary under different environmental conditions, although they can also be enhanced by various cultural production practices (Thomson et al. 2018; Steyn et al. 2005).

In most flowering plants, fruit red skin color levels tend to develop most strongly during ripening (Thomson et al. 2018). Some pear cultivars, such as 'Bon Rouge' (a mutant of 'Bartlett'), 'Flamingo', and 'Rosemarie' appear to deviate from this pattern as they attain their maximum anthocyanin levels midway between anthesis and harvest. From then on, anthocyanin synthesis decreases slowly until harvest time in response to light, temperature, solar radiation, and competition for assimilates (Steyn et al. 2005; Thomson et al. 2018). Color development in pears either requires or is enhanced by light intensity, and wavelength (Thomson et al. 2018).

Dramatic drops in temperature as well as low temperatures promote increases in transcript levels of five anthocyanin biosynthetic genes involved in the anthocyanin biosynthesis pathway, and thereby inducing red skin color development (Ubi et al. 2006). On the other hand, high temperatures reduce anthocyanin biosynthesis through down-regulation of regulatory gene transcription factors for anthocyanin production, including those of *MYB*, *bHLH,* and *WD40* (Steyn et al. 2005; Thomson et al. 2018) which can also reduce the stability of existing anthocyanins (Mori et al. 2007). Anthocyanin degradation and color loss are reported to increase linearly between 10 and 30 °C (Steyn et al. 2005), more so in 'Rosemarie' because of its lower capacity to synthesise anthocyanin (Steyn et al. 2004). Higher concentrations of anthocyanin provide a buffer for color loss before high temperatures visibly affect red coloration of fruit skin (Steyn et al. 2004). Conversely, high-colored cultivars, such as 'Bon Rouge' and 'Flamingo', do not respond to low temperatures for anthocyanin synthesis, while 'Rosemarie' does.

It has been reported that in *P. communis*, high red fruit skin color pigmentation is attributed to spontaneous bud mutations of green-skinned cultivars, including 'Bartlett', 'Comice', and 'Beurré D'Anjou', wherein not only the fruit skin is red, but also those of leaves, especially of new shoot growth (Booi et al. 2005). Often, these mutations are not stable, and some tissues of a tree, such as leaves and fruit, can revert back to the original phenotype (Booi et al. 2005). Nevertheless, stable mutants of these cultivars have been commercialized, such as 'Max Red Bartlett', 'Bonne Rouge', and 'Sensation', all sports of 'Bartlett'. However, many red mutants released commercially, including 'Crimson Gem', a red 'Comice', have had limited success because of poor tree vigor and cropping (Dondini and Sansavini 2012). Furthermore, mutagenesis has also been used to develop commercial cultivars of 'Bartlett' with red skin pigmentation, such as 'Homored' (Dondini and Sansavini 2012). The red tissue color induced by such mutations is controlled by a major dominant gene with a simple 1:1 segregation ratio for red:green seedlings, for both leaf and fruit phenotypes, thus

indicating Mendelian inheritance for this trait (Booi et al. 2005). Subsequently, this red color has been mapped to LG4 using a simple sequence repeat (SSR)-enriched map of an 'Abbé Fétel' × 'Max Red Bartlett' seedling population (Pierantoni et al. 2004; Dondini et al. 2008).

Pierantoni et al. (2010) have mapped *PcMYB10*, which encodes an R2R3-MYB transcription factor involved in the control of the anthocyanin biosynthetic pathway, onto LG9 of both 'Abbé Fétel' and 'Max Red Bartlett'. This corresponds to the same location as *MdMYBa* and *MdMYB10* that control red color pigmentation in fruit skin of apple (Espley et al. 2007). The pear transcription factor *PyMYB10* gene, a likely ortholog of *MdMYB10,* has been positively associated with anthocyanin biosynthesis in ripening fruit of red-skinned pear, and its function has been confirmed (Feng et al. 2010; Yao et al. 2017). Yet, another transcription factor, *PyMYB114,* has been identified on LG5 of Chinese pear (*P.* × *bretschneideri*), and its abundance, correlated with *PyMYB10* in enhancing anthocyanin biosynthesis, is confirmed when co-transformed in both tobacco and strawberry (Yao et al. 2017). Kumar et al. (2017) have also identified a SNP associated with red skin phenotype on LG9, but it is unclear whether or not it is associated with *PcMYB10*. Recently, Ntladi et al. (2018) have mapped a major QTL near the telomeric region on LG9 of 'Abbé Fétel' that is associated with genes MYB21 and MYB39, which is found to be responsive to environmental changes, and varies between years.

Breeding programs have used a range of red-skinned bud sports, such as 'Max Red Bartlett', 'Red Sensation', and 'Rosired', as parents to transfer the red color pigmentation to new cultivars (Dondini and Sansavini 2012). Earlier, it has been reported that phenotypic selection for red leaf color is possible in segregating seedlings of young nursery plants (Booi et al. 2005), and that it is easy for breeders to identify seedlings carrying the dominant gene for red color without using marker-assisted selection (MAS). However, seedlings carrying a gene for red skin color, developed from red-skinned sports, develop leaves and fruit with varying intensities of red color pigmentation (Volz et al. 2008). Some mutants, such as 'Starkrimson', derived from 'Clapp's Favorite', are not capable of transferring red fruit skin coloration to their progeny as the mutation is only present in the epidermis, i.e., the germ layer does not carry the mutation (Bell et al. 1996).

Some genetic sources for red fruit skin color in both Asian and European cultivars are totally dependent on solar radiation and light to induce red blush development on fruit (Zhang 2012; Steyn et al. 2005). Therefore, presence of a gene (s) controlling red skin color from these sources cannot be inferred from red leaf color of seedlings. In a New Zealand study, segregation ratios of 5(non-blush):3(red blush) for fruit blush, derived from *P. pyrifolia* cv. Huobali, are observed in four seedling populations; whereas, segregation ratios of 3(non-blush):1(red blush) are obtained in three other seedling populations. Furthermore, when both parents are descendants of 'Huobali', segregation ratios of 3(non-blush):5 (red blush) in four seedling populations and 7 (non-blush):9(red blush) in three other seedling populations have been observed. These segregation ratios indicate that a complementary two-dominant gene control mechanism is present, wherein both genes are required for color development. A similar segregation pattern for red blush color fruit may also be observed for seedling populations involving *P. communis* cv. Louis Bonne de Jersey, an old French cultivar with red blush fruit (Volz et al. 2008). However, different segregation ratios have been observed at the Zhengzhou Fruit Research Institute (ZFRI) in China in crosses wherein both parents, 'Mantianhong', derived from 'Huobali', and 'Hongxiangsu', derived from 'Korla Pear', have red skin color fruit. Segregation ratios of 3(non-blush): 2 (red blush) and 9(non-blush):8(blush) in seedling populations of 'Mantianhong' × 'Hongxiangsu' and 'Yuluxiang' × 'Mantianhong', respectively, have suggested that the red skin color trait is controlled by a single dominant gene that tends toward green-skinned segregation (Xue et al. 2017a).

In the above Zhengzhou studies, red skin coloration mapped to a 111.9–177.1 cM QTL interval on LG5 (Xue et al. 2017a). This is a different chromosomal location to the dominant gene derived from the European pear 'Bartlett' which is mapped to LG4 (Dondini et al. 2008). Recently, Ntladi et al. (2018) have also identified two SSR markers, NB101a and SamsCo865954, that are closely associated with a major QTL for skin blush on LG5 in 'Flamingo'. These markers are present in approximately 90% of seedlings that scored a high blush level. Thereby, two candidate genes, MYB86 and UDP-glucosyltransferase, have been identified. Earlier, in an F1 population of 102 individuals from a cross of 'Bayuehong' ('Clapp's Favourite' (red sport) and 'Zaosu') × 'Dangshansuli', QTLs for control of red skin color have been mapped to LGs 4, 13, and 16 (Wu et al. 2014). Interestingly, the QTL on LG4 is located at 4.8 cM (Wu et al. 2014), differing from that mapped for 'Bartlett' at 64 cM (Dondini et al. 2008), while QTLs for red blush are located on LG13 or LG16, and are deemed to be novel. Collectively, these results suggest that additional research to elucidate these different loci controlling red color in pear along with their interactions must be conducted.

It is critical to point out that breeding for either full-red or blushed fruiting pear cultivars for hot climate regions is challenging, as fruit skin color loss, close to harvest time, can be high. Therefore, it is important to choose cultivars with the highest anthocyanin levels and fruit blush as parents in breeding programs to minimize the likelihood of anthocyanin degradation due to hot temperatures and intense light exposures in these environments (Steyn et al. 2004). In the joint Spanish Institut de Recerca i Tecnologia Agralimentàries (IRTA)/PFR breeding program, selection of parents with high levels of red color and carrying more than one source of red color genes have been successful in developing pear cultivars that retain high levels of red color at harvest time under Spanish growing conditions (Batlle et al. 2008).

It has been recently reported that very good breeding progress can be made by using parents that both carry more than one source of red color gene(s), as heritability is then found to be high ($h^2 = 0.86$) for red color fruit (Kumar et al. 2017). Once crosses are made using parents carrying multiple sources of red skin fruit color, MAS would be beneficial in identifying seedlings carrying specific sources of red color.

4.3.5 Fruit Russet

Unlike many other fruits, the presence of russet on fruit is acceptable for fresh market pears, as long as russet is smooth, and ideally, fully covering the skin (Bell et al. 1996). Russeting of the fruit pericarp is attributed to accumulation of a cork layer resulting from suppressed biosynthesis of suberin, cutin, and wax, and this layer can be either green or brown in color (Wang et al. 2014). Inoue et al. (2006) have obtained a 3:1 segregation ratio for russet:non-russet and partial russet fruit in an F1 seedling population where both parents have russeted fruit skin, and a 1:1 ratio in an F1 seedling population derived from fully russeted and partially russeted parents. White et al. (2000b) have calculated a low heritability ($h^2 = 0.16$) for russet in ten European pear seedling populations; however, when five Asian and interspecific crosses are included, the heritability is found to increase ($h^2 = 0.55$). This finding is similar to heritability values reported earlier (Bell and Janick 1990), as well as in a GBS study of European, Asian, and interspecific germplasm (Kumar et al. 2017).

Early on, Kikuchi (1924, 1930) has proposed that pear fruit russet is controlled by two loci, *R* and *I*. More recently, it is hypothesized that the *R* locus has a dominant effect on cork layer development, and the modifier locus I has a dominant effect on russet suppression (Saito 2016). In this proposed model, *RR* genotypes are completely russeted, *Rrii* are partially russeted, and *RrI* are partially russeted when environmental conditions are ideal (Hancock and Lobos 2008). A major QTL for russet has been identified on LG8 (Yamamoto et al. 2014; Kumar et al. 2017; Inoue et al. 2006).

4.3.6 Fruit Skin Friction Discoloration (Scuffing)

Marking of fruit skin (scuffing) during post-harvest handling operations and in the supermarket following cold storage is a serious problem for many commercial pear cultivars, as this downgrades fruit quality and discourages purchase (Brewer et al. 2011; Saeed et al. 2014). The mechanism causing scuffing involves a combination of physical stress and biochemical reactions, in particular enzymatic oxidation of polyphenols by polyphenol oxidase (PPO) (Saeed et al. 2014). Harvest maturity can influence scuffing susceptibility, although this trait is genotype dependent (Saeed et al. 2014).

Analysis of interspecific seedling populations derived from European and Asian pedigrees has revealed that scuffing has a high narrow-sense heritability of $h^2 = 0.72$ with a high correlation between years (Brewer et al. 2011). Using germplasm accessions of similar, but wider genetic backgrounds, a subsequent GBS study has confirmed this observed high heritability ($h^2 = 0.61$) and year-to-year repeatability (Kumar et al. 2017). It has been reported that susceptibility to low-scuffing is derived from Asian pear (Brewer et al. 2011), and this is supported by a finding that the largest effect SNP allele associated with scuffing is present in Asian but absent in European pear accessions (Kumar et al. 2017). Scuffing is a complex polygenic trait as highlighted by the identification of 105 QTLs associated with 22 relevant fruit traits, including those of average scuffing score, fruit firmness, polyphenoloxidase (PPO) activity, ascorbic acid concentration, and production of 17 polyphenolic compounds (Saeed et al. 2014). With this many small-effect QTLs distributed over 11 chromosomal regions (LGs 2, 3, 4, 7, 9, 10, 11, 13, 14, 15, and 16), it is suggested that genomic selection is better suited in identifying scuffing-resistant individuals early in the breeding cycle. In a GBS study, Kumar et al. (2017) have identified a SNP for scuffing on LG15.

4.4 Tree Production

Cultivars that produce many branches; i.e., 'feathering', naturally facilitate clonal propagation of trees by nurserymen, especially for those trees that will be planted in traditional orchard systems, wherein within-row planting distances are wider than those of closely planted systems. European pear cultivars 'Conference' and 'Abeté Fetel' produce high numbers of feathers in contrast to 'Passe Crassane' (Dondini and Sansavini 2012) and to Asian cultivars. Some Asian cultivars and interspecific hybrids develop few branches along with very upright-growing shoots. This suggests that heading of young trees planted in a nursery or an orchard, along with use of plant growth regulator treatments may be required to induce feathers. Currently, an understanding of the genetic factors controlling feather/shoot production is lacking.

4.4.1 Precocity

As perennial fruit trees have long juvenile periods, reducing this juvenility period is very important for all these breeding programs (Brewer and Palmer 2011). Pears grown commercially in countries like New Zealand must be competitive with apples in terms of speed to production (Brewer and Palmer 2011). Progress can be made in breeding for a reduced juvenile period in pears as this trait is under additive genetic control (Bell et al. 1996), and there is a positive correlation between length of the juvenility period and precocity of selections propagated onto rootstocks.

In general, seedlings of *P. pyrifolia* are more precocious than those of *P.* × *bretschneideri* and *P. communis* (Bell et al. 1996). Selection of parents for reduced juvenile period and increased precocity over several generations in the New Zealand program has enabled development of seedlings that can come into fruiting within three years following crossing in some interspecific hybrid progenies.

4.4.2 Harvest Season

Extending the harvest season will maximize use of grower and packing house resources and will support efforts in meeting market needs (Dondini and Sansavini 2012; Bell et al. 1996; Brewer and Palmer 2011; Saito et al. 2015). Although there is a high demand for the first fruit of the new season, many early season pear cultivars have poor fruit quality, small fruit size, uneven ripening, and short storability due to internal breakdown (Bell et al. 1996; Dondini and Sansavini 2012; Saito 2016). In an Asian pear seedling population, Abe et al. (1993) have observed a high positive correlation between mid-season ripening parents and fruit weight. Furthermore, the presence of a strong link between high ethylene production and early maturity in Japanese pear cultivars explains their observed poor storability (Itai et al. 2003).

It has been reported that fruit harvest date is a polygenic trait, with low environmental influence (Abe et al. 1993). A high heritability for ripening date, h^2 values of 0.80–0.95, has been reported in seedling populations of Asian heritage (Nishio et al. 2011; Abe et al. 1993). This has been further confirmed in a recent study wherein heritability of $h^2 = 0.83$ has been reported (Hae-Sung et al. 2015). On the other hand, moderate heritability ($h^2 = 0.49$) for ripening date has been reported in seedlings of late ripening parents of European pear heritage (Bell et al. 1996).

QTLs controlling harvest date have been identified at the bottom of LG3 (nearest marker: *BGA35*) and at the top of LG15 (nearest marker: *PPACS2*) of 'Taihaku' (Yamamoto et al. 2014). The *PPACS2* probe for an ACC synthase coding gene, identified in a DNA band of 0.8 kb in length, is found to be specific to *P. pyrifolia* cultivars producing moderate ethylene levels during ripening and storage (Saito 2016; Itai et al. 1999). Recently, Ntladi et al. (2018) have detected a QTL on LG9 of 'Flamingo' explaining more than 30% of the phenotypic variance, with 88% accuracy, for seedlings flowering earlier than either parent in a progeny of 'Flamingo' 'Abate Fetel'.

Given the moderate to high heritability for fruit ripening date reported above, choice of parents in breeding for early or late fruit ripening is important. If both parents are early season cultivars, a greater proportion of their progeny will have this desired trait (Bell et al. 1996). Similarly, if both parents are late-season cultivars, a larger proportion of their progeny will mature later in the season, as compared with progeny from one early- and one late-season parent (Bell et al. 1996). Newly improved early season European pear cultivars that have been released from Italian breeding programs include 'Etrusca', 'Sabina' (Bellini and Nin 2002), 'Tosca', 'Norma', and 'Carmen' (Rivalta et al. 2002), while in Japan, 'Hatsumaru' with fruit quality equivalent to 'Kosui' has recently been released (Saito 2016).

4.4.3 Parthenocarpy

Parthenocarpy, development of fruit without fertilization of ovules and rendering fruit seedless, is a useful commercial trait of European pear. This is especially important in some pear-growing regions in Europe whereby early spring frosts and adverse conditions can prevent effective pollination. It is reported that in some growing environments wherein pear cultivars are capable of developing parthenocarpic fruit, pollinators are not deemed necessary (Bell et al. 1996; Nishitani et al. 2012).

In a study investigating parthenocarpy in 31 accessions of several pear species, including *P.* × *bretschneideri*, *P. ussuriensis*, *P. pyrifolia*, *P. communis,* and interspecific hybrids, it is found that five tested European pear cultivars have consistently set fruit, and the fruit has enlarged size in the absence of pollination (Nishitani et al. 2012). Some Chinese and European cultivars, such as 'Mili', 'Wowoli', 'Alexandrine Douillard', 'Bartlett', and 'La France' are found to have partial compatibility when self-pollinated. Moreover, it is observed that Chinese and Japanese cultivars do not demonstrate consistent and stable fruit set without fertilization when compared to European

cultivars. Among these cultivars, 'La France' is deemed the best-performing cultivar, as non-fertilized fruit weighed only slightly less than pollinated fruit. Furthermore, it is observed that fruit weight and size of non-fertilized fruit are inherited, thus it should be possible to transfer this parthenocarpy trait from the European pear cultivar La France to Japanese or Chinese pears (Nishitani et al. 2012).

It has been reported that three phenylpropanoid pathway-related genes are found to be either up- or down-regulated in highly parthenocarpic pear cultivars (Nishitani et al. 2012). Therefore, breeding for parthenocarpy may be accelerated by using molecular markers for these three genes once these markers are developed and validated across species (Nishitani et al. 2012). However, parthenocarpy is a low priority in most Asian pear breeding programs (Nishitani et al. 2012), as absence of seeds in parthenocarpic fruits is associated with lower fruit flavor and lower soluble solid concentrations (Bell et al. 1996).

4.5 Adaptation to Abiotic and Biotic Stresses

4.5.1 Low-Chill Requirement

Temperate zone cultivars are not well adapted for regions with subtropical climates, wherein chill requirement, necessary to achieve adequate flowering, is often unmet. Breeding for adaptation for low-chill requirement, i.e., flowering after fewer chilling hours, is one approach to develop cultivars with satisfactory yields and acceptable fruit quality in regions with warmer climates. As time of bud break is not a good indicator of chilling requirement, it is preferable to screen seedling trees for number of buds breaking (Rumayor et al. 2005).

Japanese pear cultivars (*P. pyrifolia*) require approximately 800 chill hours to break dormancy (Yamamoto et al. 2010); whereas, the estimated minimum chill hour requirement at 3 ± 1 °C for some European pears such as 'Rocha', 'Packham's Triumph', and 'Forelle' is 750 h, while for others, such as 'Winter Bartlett', 'Red Bartlett', and 'Max Red Bartlett', approximately 1050 h of chilling is required (Kretzschmar et al. 2011). The majority of pear cultivars adapted to subtropical growing conditions belong to *P. pyrifolia.* While most European pear cultivars are not well adapted to these growing conditions, there are a few exceptions. These exceptions include 'Hood' and 'Flordahome' (requiring 250 chill hours between 3–5°C), both are hybrids between *P. communis* and *P. pyrifolia*. 'Flordahome' has been developed and released from the University of Florida breeding program in 1982 (Sherman and Lyrene 2003).

Interspecific hybridizations between *P. pyrifolia* and *P. communis* have been used to develop low-chill European pears; however, fruit quality of low-chill *P. communis* cultivars, such as 'Kieffer' (550 chill hours between 3 and 5 °C), 'Le Conte' (450 chill hours between 3 and 5 °C), and 'Garber', is low (Hauagge and Cummins 2013; Abd El-Zaher et al. 2015). Interestingly, F1 seedling populations in a Mexican pear breeding program have resulted in seedlings with chill requirements ranging from 0 to 500 chill hours (Rumayor et al. 2005). Moreover, evergreen types have been identified from an open-pollinated seed population of 'Hood', as these seedlings do not require low temperatures to break dormancy (Rumayor et al. 2005). Finally, breeders in Egypt have used 'Hood', 'LeConte', and 'Yali' in crosses, and have selected a range of seedlings requiring fewer than 200 chilling hours at 7 °C (Abd El-Zaher et al. 2015; Stephenson 2015; Barbosa et al. 2013).

4.5.2 Cold Hardiness

Pears are grown in many parts of the world where temperatures can drop low enough to cause cold injury to shoots, spurs, trunks, and roots that may result in tree death. Plant cold hardiness is a complex trait, as it is influenced by temperature, day length, and plant physiological status (Palonen and Buszard 1997). Thermal analysis can be used for measuring cold hardiness for some pear tissues (Quamme 1991).

However, breeding for cold adaptation is best undertaken under actual growing environments, which may include Northern regions of the USA, Canada, Europe, Russia, and Mongolia. Although genetic progress has been made, and pear cultivars have been developed that can withstand winter temperatures as low as −30 to −40 °C, fruit quality is not deemed as satisfactory as those commercial cultivars grown in major pear-growing regions (Bell 1991).

Low spring temperatures, particularly early spring frosts, often cause flower damage and crop loss. As flower buds do not supercool, the earlier a cultivar flowers, the greater the risk of spring frost damage (Bell et al. 1996; Palonen and Buszard 1997). Breeding for late flowering to avoid frost or to promote parthenocarpy is an option, as bloom date is highly heritable, but noting that late flowering is not linked to late fruiting (Quamme 1991; Palonen and Buszard 1997).

Although inheritance of cold hardiness has not been investigated in pear, it has been reported that cold hardiness in apple is under polygenic control with additive effects, and with little evidence for incidence of epistasis and dominance (Bell et al. 1996). A range of pear cultivars have been classified for their vulnerabilities to winter injury based on cold damage to xylem and frost injury to buds. In general, it has been reported that pear xylem and flower bud hardiness are not highly correlated (Bell 1991; Bell and Itai 2011).

4.5.3 Disease and Pest Resistance

The genus *Pyrus* is susceptible to damage from various numbers of diseases and pests (Bell et al. 1996). The importance of a specific pest or disease in any particular region will be dictated by the cost of control management as well as the detrimental economic impact on the crop, particularly whereby control is less than fully effective. In some cases, susceptible cultivars are excluded from certain regions due to devastating effects of a pathogen or pest on tree productivity and fruit quality.

Screening for genetic resistance to a pest or disease in a germplasm collection to develop new cultivars with either higher tolerance, or ideally, resistance is an attractive proposition for any pear breeding program. The long-term efficacy of resistance should be carefully considered, as breakdown of resistance by different strains of the pathogen or pest can occur (Bus et al. 2011). Therefore, breeding for durable resistance using multiple resistance genes should be a long-term goal for pear breeding programs, as it is already the case for apple (Bus et al. 2011).

Fruit quality breeding objectives, mentioned in earlier sections, should not be ignored while breeding for disease/pest resistance as no matter how strong and effective the resistance of a cultivar, consumer's interest is mainly focused on fruit attractiveness and eating quality. The genetic background conferring resistance/s should also be taken into consideration. For pear, the breeding cycle is at least 5 years, and evaluation before cultivar release can take in excess of 15 years. Thus, introgression of resistance genes carried by large-fruited eating cultivars and land races of *P. communis*, *P. pyrifolia*, *P.* × *bretschneideri,* and *P. ussuriensis* into new cultivars would yield high fruit quality more readily than introgression of resistance genes from small-fruited *Pyrus* species of poor fruit quality. More specifically, in breeding of European pears, introduction of resistance genes from other European pears is highly desirable, and equally, introduction of resistance genes from Asian species is more suitable in breeding for Asian pears.

This section of the review concentrates on current status of breeding for resistance to the three major diseases of pear, including fire blight, pear scab, and black spot, as well as for the important economic pest of pear psylla (Psylla).

4.5.3.1 Fire Blight Resistance

Fire blight, caused by the bacterium *E. amylovora* (Burrill) Winslow et al., is a serious disease of pear, and indeed of various other Rosaceae species (Van der Zwet et al. 2012). This disease originated in the USA, and has been first reported in 1718 in the Hudson Valley, New York. Since

then, it has spread throughout every region of the USA, as well as throughout Europe, Middle East, Oceania (New Zealand), and has recently been detected in Kurdistan and South Korea (Park et al. 2017). The most common commercial cultivars grown today in North America and in Europe are known to be either susceptible, such as 'Bartlett', 'Abate Fetel', 'Beurré D'Anjou', 'Beurré Bosc', 'Comice', or only moderately resistant such as 'Conference,' to fire blight. These cultivars are grown in regions where climates are not very conducive for fire blight disease development, so growers are able to manage the disease somewhat satisfactorily.

Over the last 40 years, efforts have been undertaken to evaluate and assess fire blight resistance status of *Pyrus* germplasm (Bell et al. 1996; Bell and Itai 2011; Peil et al. 2009; Van der Zwet et al. 2012). While total immunity to fire blight has not been observed, high levels of resistance have been identified in some pear species. The proportion of resistant material in European, circum-Mediterranean, and Central Asian species tends to be lower than that found in East Asian species. However, Van der Zwet et al. (2012) have scored 14 of 75 'popular commercial' European pear cultivars and 24 of 76 Asian/Oriental pear as 'most resistant.' Since the year 2000, several new *P. communis* cultivars have been released that are reported to have high levels of fire blight resistance (Dondini and Sansavini 2012; Hunter and Layne 2004).

Screening methods used to determine fire blight resistance of cultivars, breeding selections, and hybrid seedlings have been reviewed extensively (Bell et al. 1996; Peil et al. 2009). Long-term field assessments are required to confirm a genotype's fire blight status, and a standardized scoring system for rating fire blight infection of trees has been developed. However, there can be substantial non-genetic variability in these assessments; hence, breeders have endeavored to control the timing and entry point of fire blight inoculum to improve assessment of inherent resistance. Artificial plant inoculations and/or use of greenhouse/plastic tent facilities to optimize environmental conditions are now commonplace in breeding programs. Where clonal replicates of a genotype are screened, frequency and severity of infection can be determined and are combined to yield a calculated index of fire blight susceptibility.

*M*ost strains of *E. amylovora* isolated from apple are capable of infecting pear and vice versa (Momol and Aldwinckle 2000). While this bacterium is a relatively genetically homogenous species (Khan et al. 2012), there is a diversity in pathogenicity among different *E. amylovora* strains (Cabrefiga and Montesinos 2005; Wang et al. 2010; Smits et al. 2017). However, unlike in apple (Norelli et al. 1984), to date there is no evidence that differential responses of the pathogen to different resistant pear genotypes exist. Pear genotypes with varying degrees of resistance to fire blight have been inoculated with several different strains of the pathogen, including some that have been previously shown to be differentially virulent on apple. While differences in host resistance and strain virulence have been confirmed, no interactions between host and strain have been observed (Quamme and Bonn 1981; Bell et al. 1990; Bell and Van der Zwet 1996). This has led to the conclusion that differentially virulent strains do not need to be considered in breeding for fire blight resistance in pear, at least in the USA (Bell and Van der Zwet 1987). Nevertheless, given that differentially virulent *E. amylovora* strains have developed against fire blight-resistant apple cultivars, it seems advisable to aim for durable fire blight resistance in pear by incorporating multiple disease resistance genes into pear breeding programs.

The genetics of fire blight resistance first received attention in the USA in the 1960s, when segregation for resistance in breeding progenies, mainly of interspecific Asian × European hybrids, derived from parents of known resistance were observed. No immunity was detected in any pear genotype, and segregation of seedlings for necrotic lesions of shoots following inoculation generally followed a continuous pattern. This suggested that inheritance for resistance was quantitative with presence of several resistance genes, and there was no pattern of inheritance specific to a certain pear species

(Layne et al. 1968; Van der Zwet et al. 1974). Further studies reinforced the hypothesis that additive gene action was the main mechanism by which fire blight resistance was inherited in pear in the USA (Bell et al. 1977), Canada (Quamme et al. 1990), Italy (Bagnara et al. 1996), and France (Durel et al. 2004). At least 18 small-to-moderate-effect QTLs, some of which may be the same, have been identified for control of fire blight resistance in European and Asian pedigrees in three genetic mapping populations (Boksccczanin et al. 2009; Bell 2018; Montanari et al. 2016b; Dondini et al. 2004). This further confirmed earlier findings that fire blight resistance is polygenically controlled.

As considerable parent-to-parent variability in capacity to transmit resistance to progeny has been observed, fire blight resistance cannot be entirely explained by the parent's own phenotypic resistance. This supports hypotheses proposing that non-additive genetic effects may also contribute to fire blight inheritance, although major dominant resistance (Drain 1943; Thompson et al. 1962) or sensitivity (susceptibility) genes in *P. communis* (Thompson et al. 1975) are also likely involved. In genetic mapping studies, minor-effect QTLs controlling resistance have been detected in susceptible parents (Boksccczanin et al. 2009; Montanari et al. 2016b). This may explain recovery of resistant genotypes that are sometimes developed from susceptible parents (Van der Zwet 1977; Bagnara et al. 1993).

4.5.3.2 Resistance to Pear Scab

Pear can be infected by two species of *Venturia,* inciting pear scab disease. *V. pirina* Aderh. infects *P. communis,* while *V. nashicola* (Tanaka and Yamamoto 1964) infects all cultivated species of Asian pear. Each fungal species is specific to its host pear species (Abe et al. 2008; Tanaka and Yamamoto 1964), thus the economic significance of each fungal species is tightly linked to the geographic distribution of the cultivated host species. *V. pirina* occurs worldwide except for East Asia, while *V. nashicola* is restricted to China, Japan, and Korea (González-Domínguez et al. 2017).

Venturia Nashicola

Some wild species of *Pyrus* are fully resistant to *V. nashicola* (Ishii et al. 1992), but of more interest to breeders is the discovery that several commercial pear cultivars are immune to this fungal pathogen, including the Japanese pear cultivar 'Kinchaku' and the Chinese pears 'Hongli', 'Mili', and 'Cangxili'. Furthermore, it has been demonstrated that progeny generated from crosses between either 'Kinchaku' (Abe and Kotobuki 1998a) or genotypes derived from 'Kinchaku' (Terakami et al. 2006) with susceptible cultivars segregate into seedlings either with no symptoms (resistant) or with abundant sporulation (susceptible) (Abe and Kotobuki 1998a). The 'Kinchaku' resistance has been used extensively in Japanese breeding programs, and a scab-resistant cultivar, 'Hoshiakari', carrying the 'Kinchaku' resistance has been named and released (Saito 2016).

A dominant major gene (*Vnk*) controlling this scab resistance has been mapped to LG1, with one SSR marker and five STS markers found to be tightly linked to this gene (Terakami et al. 2006). Two flanking markers, used together, have accurately predicted resistant seedlings in segregating progenies derived from 'Kinchaku' (Gonai et al. 2009). These markers are currently being used in MAS for scab resistance in Asian pear breeding programs in Japan (Yamamoto and Terakami 2016).

Immunity to *V. nashicola* in European pear cultivars, including 'Bartlett' and 'La France', has been reported to be transmitted to their progeny and purported to be controlled by single dominant genes (Abe et al. 2000). Subsequent genetic studies have indicated that a QTL for resistance from 'La France' (Yamamoto et al. 2009) and a major dominant gene conferring resistance from 'Bartlett' (*Rvn2*) (Cho et al. 2009; Bouvier et al. 2012) are likely to be the same, as both mapped to the bottom of LG2. However, the scope of resistance to *V. nashicola* may not be exactly the same for each cultivar, as Yamamoto et al. (2009) have mapped a second QTL for resistance, derived from 'La France', to LG14. Furthermore, two cleaved amplified

polymorphic sequence (CAPS) markers tightly linked to *RVn2* have been developed for likely use in MAS (Cho et al. 2009).

It has been reported that non-host resistance to *V. nashicola* derived from European pears may provide broader spectrum resistance than host resistance derived from Asian pears, as they are effective against all races of the pathogen (Gill et al. 2015). Often, host resistance is race-specific, involving gene-for-gene relationships, and may be less durable. Indeed, five races of *V. nashicola,* collected from various regions in Asia, have shown differential reactions to different hosts (Zhao et al. 2012). However, use of non-host resistance from *P. communis* in Asian pear breeding may be disadvantageous, as it may incorporate less desirable alleles from European pear. Nevertheless, Kim et al. (2016) have introgressed resistance from 'Bartlett' into *P. pyrifolia* 'Whangkeumbae' to develop a new Korean cultivar, 'Greensis'.

Partial resistance to *V. nashicola* has been observed in several Asian pear cultivars and their progeny, as well as in progeny derived from European pear. Abe et al. (2000) speculated that this resistance reaction was under polygenic control. Differences in incidence of necrotic leaf tissues have been observed among commercial Korean cultivars in replicated field trials (Won et al. 2011). Four major gene loci were involved in varying necrotic resistance reactions observed in leaf inoculation studies using a segregating progeny, derived from two resistant seedlings of 'Yali' x 'Jingbaili' that have been backcrossed to their parents, susceptible cultivars 'Yali' (*P.* × *bretschneideri*) and 'Jingbaili' (*P. ussuriensis*) (Zhang et al. 2012).

Venturia pirina

Most *P. communis* cultivars have demonstrated a range of susceptibility to *V. pirina* in the field, although results have not always been consistent (Vondracek 1982; Postman et al. 2005). Hence, most scab resistance in *P. communis* is presumed to be polygenic, and recent genetic mapping in several partially resistant cultivars has confirmed this finding. For instance, resistance in 'Abè Fétel' is proposed to be controlled by two independent major QTLs on LGs 3 and 7, and collectively explaining ~88% of the observed variation in susceptibility in progeny of 'Abè Fétel' × 'Max Red Bartlett', a scab-susceptible cultivar (Pierantoni et al. 2007). A locus on LG1 confers resistance derived from 'Wilder' with a major QTL (67%) co-localized with the major gene *Vnk* on the pear genome (Perchepied et al. 2015). Recently, a major resistance gene (*Rvp1*), derived from 'Navara', has been identified on LG2 (Bouvier et al. 2012), indicating that such genes are present in *P. communis* germplasm. The SSR marker CH02b10 is mapped close to this gene. As is the case for *V. nashicola*, *V. pirina* also shows strain heterogeneity in pathogenicity to different resistance reactions present in *P. communis* (Chevalier et al. 2004). The breeding strategy in *P. communis* should aim to bring together a number of resistance QTL and major genes in order to achieve resistance durability in new cultivars.

Asian pear cultivars are generally resistant to *V. pirina* (Postman et al. 2005) and may serve as useful sources of non-host resistance in European pear breeding. However, these sources of resistance are less well understood. A major QTL is identified on LG4 from a breeding selection, likely derived from *P. pyrifolia* (Perchepied et al. 2015). Moreover, seven QTL controlling resistance (two each on LG7 and LG2, as well as one each on LG5, LG10, and LG17) have been identified in a complex interspecific hybrid family derived from *P. communis*, *P. pyrifolia,* and *P. ussuriensis* (Won et al. 2014). Furthermore, all of these QTLs have exhibited differential responses to discrete *V. pirina* isolates, except for the QTL on LG17 which is effective against all strains. However, the host/non-host nature of the QTL has not been established in this study, as not all accessions in the pedigree have been available for marker analysis.

While resistance to *V. nashicola* in leaf tissues extends to the fruit (Abe et al. 2008), this is not always the case for resistance to *V. pirina*. Some Asian and European pear cultivars (Postman et al. 2005), as well as interspecific hybrids derived from Asian and European pears (Brewer et al. 2009), have exhibited leaf resistance

reactions to *V. pirina,* but have shown some scab on fruit, thus indicating presence of a differential resistance reaction depending on tissue. Hence, reliance on leaf resistance symptoms as an indicator of total plant resistance may not always be appropriate. Further studies are warranted to develop a better understanding of resistance response of pear fruit to *V. pirina.*

4.5.3.3 Pear psylla

Pyrus hosts several species of the pear psylla (Psyllidae: Psyllinae: *Cacopsylla* spp.), but only three are of economic importance (Hodkinson 2009; Ouvrard 2017). *Cacopsylla pyricola* Foerster is the most widespread, and it is presently found in Europe, the Middle East, North and South America, Argentina, Russia, South Korea, and Japan (Ouvrard 2017). *Cacopsylla pyri* Linné dominates in Europe, but has also been reported in the Middle East and Central Asia, including China. *Cacopsylla bidens* Šulc is present in France, Italy, Greece, central Asia, including India, as well as South America (Valle et al. 2017).

The control of pear psylla in commercial pear orchards is handled by using selective pesticides along with a range of active natural predators (Trapman and Blommers 1992). However, the psylla reproduces prolifically, with multiple generations per year, and readily develops resistance to many pesticides (Civolani 2012).

All of the major commercial cultivars of *P. communis* are susceptible to pear psylla. Therefore, incorporation of resistance to this pest into new cultivars has been an important objective for several European pear breeding programs. Fortunately, partially resistant *P. communis* cultivars, originating mainly in Eastern Europe, have been identified (Bell and Stuart 1990; Sestras et al. 2009; Benedek et al. 2010; Bell 1992, 2013a), and used in some breeding programs (Branişte et al. 2008). However, transmission of resistance to progenies has often been poor (Bell 2013b). For example, the old Italian cultivar 'Spina Carpi' is resistant, but it does not transmit this resistance to its progeny (Rivalta et al. 2002). This may reflect the inherent low narrow-sense heritability of this resistance (Bell 2013b).

Immunity to pear psylla within *Pyrus* has not been documented (Quarta and Puggioni 1985; Briolini et al. 1988). However, there is a wide variation in resistance responses to *C. pyricola* among *Pyrus* species, first documented in North America by Westigard et al. (1970) and Quamme (1984), and well summarized by Bell and Itai (2011). East Asian pear species are generally resistant, whereas mid-Asian, Mediterranean, and European species exhibit a wide range of response, from susceptible to resistant.

Introgression of psylla resistance from Asian pear species into high-quality *P. communis* cultivars was initiated in the USA, back in the 1960s. It was reported that large-fruited *P. ussuriensis* material crossed with *P. communis* cv.Bartlett transferred its psylla resistance to a majority of the progeny (Harris and Lamb 1973). Subsequently, a backcrossing strategy to 'Bartlett', as well as to other *P. communis* cultivars was followed in the USA (Harris and Lamb 1973), as well as in both Italy and France (Lespinasse et al. 2008; Nin et al. 2012). Two second-generation cousin hybrids, NY10353 and NY10355, with improved fruit quality performance and resistance to *Psylla,* have been extensively used in breeding programs in the USA, Italy, and France (Pasqualini et al. 2006; Nin et al. 2012; Dondini and Sansavini 2012).

One of the major hurdles in introgressing psylla resistance into new pear cultivars has been the poor fruit quality of resistant progenitors and the seemingly difficult task of improving fruit quality in subsequent generations. Harris and Lamb (1973) have suggested that the *P. ussuriensis* source of resistance avoided some undesirable fruit quality attributes, such as small size and flesh grittiness. However, psylla-resistant selections originating from this source, as well as those derived from Eastern European-resistant *P. communis* cultivars, have not exhibited the quality required of a modern new pear cultivar (Bell 2013b). Thus far, no cultivar has yet been released from these breeding efforts.

It has been reported that psylla resistance from *P. ussuriensis* seems to be under polygenic control (Lespinasse et al. 2008). A major QTL for control of pear psylla located on LG17 of a pear selection, NY10355 (Bouvier et al. 2011), has been confirmed along with two additional QTLs located on LG1 and LG4. A strong epistatic interaction has been observed between the latter QTLs and that on LG17 (Perchepied et al. 2016). Nearly all of the genetic variation in psylla nymph infestation is explained by these QTLs. The major resistance QTL on LG17 has also been identified in segregating progeny of NY10353 (Dondini et al. 2015). The SSR markers CH05G03 (Dondini et al. 2015) and NB126a-2 (Perchepied et al. 2016), closely linked to the QTL controlling resistance on LG17, have been identified from NY10353 and NY10355, respectively, and provide a first step in developing promising resources for MAS.

In other efforts, a *P.* × *bretschneideri* × *P. communis* hybrid that is partially resistant to *C. pyri* is reported to transmit psylla resistance to its progeny when crossed with the *P. communis* cultivar 'Moonglow' (Montanari et al. 2015). This resistance, most likely to be derived from 'Xuehauli', is different from those of other *P. ussuriensis* lines as a QTL for resistance is located on LG8, but not on LG17. This QTL explains up to 30 to 39% of the observed phenotypic variation in total numbers of psylla nymphs. Further, this QTL is found to be stable over two years of testing, along with an SSR marker, CH05a02, that is closely associated with this QTL. Several other minor QTLs for resistance, located on LG5, 11, and 15 (from 'Moonglow'), have also been identified, but these are not stable over years of testing, and their significance is inconclusive. Some interspecific hybrids of susceptible *P. communis* × resistant *P. pyrifolia* have also shown resistance to psylla, but the genetic mechanisms of these resistances are yet unknown (Robert and Raimbault 2005; Pasqualini et al. 2006).

It is unknown if different biotypes of pear psylla exist that can overcome any of the above reported resistances. Puterka (1997) has found that *C. pyricola* collected from five regions in the USA has demonstrated similar responses to both susceptible and resistant pear germplasm from different sources. Interestingly, the *P. ussuriensis*-derived resistance line developed in the USA for *C. pyricola* is also resistant to *C. pyri* in Europe (Robert and Raimbault 2005; Pasqualini et al. 2006), as well as to *C. bidens* in Israel (Shaltiel-Harpaz et al. 2014). These reports suggest presence of a relatively broad-spectrum resistance for pear psylla. Nevertheless, given the rapid development of pesticide-resistant strains of pear psylla over the last few decades (Civolani 2012), breeding should aim for resistance that is durable through pyramiding of different QTLs for resistance (Corwin and Kliebenstein 2017).

The modes of host resistance to pear psylla have been studied extensively for several resistance sources (Bell and Puterka 2004). Both nymphal feeding antixenosis (unpalatability) and nymph antibiosis (mortality) are deemed important, but ovipositional antixenosis is less important for tested resistant selections derived from both *P. ussuriensis* and *P. communis*. In contrast, *P.* × *bretschneideri* resistance, derived from 'Xuehauli', is attributed to both antibiosis and ovipositional antixenosis (Montanari et al. 2015). To date, mapping studies have not yet conclusively revealed the presence of specific QTLs associated with each of these different modes of resistance (Montanari et al. 2015). Further investigation is needed to better understand the genetic mechanism of these different components of *Pyrus* resistance to pear psylla in order to identify better resources for developing psylla-resistant cultivars.

In summary, there is a reasonable understanding of the genetics of the major scab resistance gene *Vnk* for *V. nashicola,* and molecular markers linked to this resistance are being used in some Japanese pear breeding programs. Furthermore, numerous sources of resistance to *V. pirina*, fire blight, and pear psylla have been identified, and these have been used in various pear breeding programs. However, in contrast to *V. nashicola* resistance, these sources of resistance have more complex genetics that is not well documented. Efficient and effective

incorporation of these various genes for resistance to these different diseases and pest into future pear cultivars can only be enhanced following thorough understanding of their genetics involved in these traits, as well as subsequent development and application of their associated molecular markers.

4.6 Rootstock Breeding

Pear growers have a limited number and range of clonal rootstocks to choose from when designing a new orchard, compared with their apple counterparts. This range is even more limited if a vigor-controlling rootstock is required, as dwarfing rootstocks equivalent to the precocious flowering and high-yielding apple rootstock 'Malling 9' are lacking (Knäbel et al. 2015; Brewer and Palmer 2011). Rootstock options for pear growers include several *Pyrus* species and alternatives from other species, such as *Cydonia oblonga* (quince), *Amelanchier alnifolia* (serviceberry), *Actaea spicata (baneberry)*, *Amelanchier canadensis (juneberry), Amelanchier lamarckii (juneberry)*, *Sorbus aucuparia* (mountain ash), *Sorbus alnifolia* (alder-leafed whitebeam), and *Pyronia veitchii* (*C. oblonga* × *P. communis*) (Elkins et al. 2012; Postman 1994).

4.6.1 Quince—*Cydonia oblonga*

Quince rootstocks are preferred in Europe because of their strong vigor control and precocity of the pear scion, as well as ease of propagation (Brewer and Palmer 2011; Necas et al. 2016). However, these have several limitations to more widespread use, including lack of cold hardiness, limited fire blight resistance, scion incompatibility, and susceptibility to iron chlorosis (Elkins et al. 2012). There has been limited breeding of quince rootstocks to address these issues (Brewer and Palmer 2011).

Scion vigor-controlling rootstocks include the semi-dwarfing 'BA29' (60% of tree size compared to that of *P. betulaefolia* seedling rootstock) (Elkins et al. 2012), developed at the French National Institute of Agricultural Research (INRA) and released in 1967 (Simard et al. 2004), the dwarfing 'Quince A' (QA), and the dwarfing 'Quince EMC' (QC) rootstocks, both released from East Malling Research Station in the United Kingdom in the 1920s (Anon.). Graft compatibility testing of pear cultivars on Quince rootstocks have suggested that 'Beurré D'Anjou', 'Comice', 'Old Home', 'Beurré Hardy', 'Flemish Beauty', 'Abbé Fetel', 'Passe Crassane', and 'Maxine' are compatible, but 'Bartlett', 'Beurré Bosc', 'Winter Nelis', 'Clapp's Favourite', and 'Forelle' are not (Lombard and Westwood 1987). Since the release of 'BA29', QA, and QC, the Quince Eline® rootstock has been released by Boomkwekerij Fleuren in Belgium. Quince Eline®, originated from a Romanian breeding program, has been developed for increased frost resistance. This rootstock is comparable to QC for scion vigor and fruit size, and it is reported to have good graft compatibility with most pear cultivars, along with frost resistance to temperatures of about −25 °C (Anon.; Brewer and Palmer 2011). In 2001, East Malling has released 'QR193/16' (EMH), originally claimed to control scion vigor similar to that of QC; however, further research has indicated that vigor control ranges between that of QC and QA (Webster et al. 2000). Although EMH contributes to good fruit size development and has good stool bed performance, it shows poor precocity relative to QC, and it is susceptible to fire blight (Brewer and Palmer 2011). EMH has been selected from seed presumed to have originated from Transcaucasia. Research efforts at the University of Pisa in Italy on breeding rootstocks tolerant to calcareous soils have led to the release of the selection 'Ct.S 212'; however, this is not resistant to fire blight, and more recently has demonstrated some inconsistency in fruit production of grafted scion cultivars (Brewer and Palmer 2011).

In a quest for developing more dwarfing quince rootstocks that have cold resistance, a large number of accessions have been selected

from the National Clonal Germplasm Repository at Corvallis (Oregon, USA) and have been screened for cold hardiness. A total of 22 quince selections have been found to be as hardy, or hardier, than standard commercial *Pyrus* rootstocks, including 'Old Home' × 'Farmingdale 87' and 'Old Home' × 'Farmingdale 97', surviving temperatures as low as −30 °C. Among these, the ten best-performing selections are currently being evaluated in research programs in Wenatchee (Washington State) and Hood River (Oregon) in the USA (Warner 2015). The best-performing rootstocks for cold tolerance have originated from Armenia, Turkmenistan, Russia, Uzbekistan, the Russian Federation, Georgia, and France, with the most cold resistant being *C. oblonga*-Arakseni, 'Avia' from Gebeseud, and 'Akhtubinskaya', an open-pollinated seedling 4 (Einhorn et al. 2017; Anon.).

4.6.2 *Pyrus*

Pyrus rootstocks are the preferred choice in North America, Asia, and Australia. A wide range of species have been used in breeding programs or in commercial orchards, including *P. communis*, *P. betulaefolia* Bge., *P. calleryana* Dcne., *P. pashia* D. Don, *P. xerophila* Yu, *P. ussuriensis* Maxim, *P. heterofolia*, *P. nivalis*, *P. longipes*, and *P. pyrifolia* Nakai (Brewer and Palmer 2011; Tamura 2012; Teng 2011; Simard et al. 2004). *Pyrus* rootstocks have good graft compatibility, a satisfactory range of cold adaptation, and can grow well in low to high pH soils. However, they have limited vigor control and precocity induction of the scion, varying levels of tolerance to *Candidatus* Phytoplasma pyri (inciting pear decline), and are generally difficult to propagate (Brewer and Palmer 2011). A continuing challenge for pear rootstock breeders is to combine vigor control and precocity of the scion, that can be obtained from Quince rootstock options, with other important traits required for a successful rootstock. This may require use of more than a single species to combine all of these required traits.

4.6.2.1 *P. communis*

P. communis is the species most widely used as a rootstock in North America, with seedlings of 'Winter Nelis' and 'Bartlett' being the main rootstocks currently used commercially (Elkins et al. 2012). However, grafted pear trees are mostly vigorous, yet they are adapted to a range of climates and soil types (Hancock and Lobos 2008). Although fire blight susceptibility is common in *P. communis,* seedling populations have been established to develop rootstocks with fire blight resistance along with some tree size reduction or dwarfing (Hancock and Lobos 2008). Globally, there are limited numbers of *P. communis* rootstocks that offer significant grafted tree size reduction. Research efforts in the USA have demonstrated that size of a grafted pear tree on 'Pyrodwarf®' is similar to that grafted on Quince 'BA29' (Brewer and Palmer 2011), and only 61–70% of that grafted on *P. betulaefolia* seedling rootstocks (Elkins et al. 2012). However, tree performance has varied depending on planting site, scion cultivar, and management practices (Elkins et al. 2012). Furthermore, yield efficiency has been poor compared to that obtained with QC, QA, and many *Amelanchier* rootstocks (Einhorn et al. 2017). In 1996, the University of Bologna in Italy has released *P. communis rootstocks* 'Fox 11' and 'Fox 16', and in 2008 has released 'Fox 9'. However, all three rootstocks are more vigorous than quince BA29 (Brewer and Palmer 2011).

From a rootstock breeding perspective, it is important to identify individuals carrying traits required as soon as possible, especially for the scion dwarfing trait. QTLs influencing expression of scion vigor and precocity have been located on LG5 and LG6 of 'Old Home' in an 'Old Home' × 'Louise Bonne de Jersey' seedling population. It is reported that the QTL on LG5 maps to a position that is syntenic to the apple 'Malling 9' *Dw1* locus located at the top end of LG5 (Knäbel et al. 2015). This QTL for rootstock control of numbers of branches produced by a grafted scion cultivar is detected in three successive years, and it is co-located with the flowering trait for total number of

inflorescences on a tree. The microsatellite marker Hi01c04, located within the QTL region on LG5, is heterozygous in both 'Old Home' and 'Louise Bonne de Jersey', and its trait association is found to be consistent over a number of years. A small-effect QTL for root suckering is also detected on LG5 within the same genomic region as that QTL for tree architecture (Knäbel et al. 2015). In the same population, QTLs have been identified on LG7 controlling development of adventitious roots on hardwood cuttings of both 'Old Home' and 'Louise Bonne de Jersey' (Knabel et al. 2017). Both of these discoveries will support efforts in developing genetic markers useful in future breeding efforts of desirable *Pyrus* rootstocks.

4.6.2.2 *P. longipes*

Rootstocks of *P. longipes* offer very good tree root anchorage, graft compatibility, and high tolerance to the bacterial canker *Pseudomonas syringae*, but provide only moderate precocity and yield efficiency, susceptibility to fire blight, and limited tolerance to pear decline (Lombard and Westwood 1987). Breeding efforts at Dresden-Pillnitz in Germany have used *P. longipes* to target improved propagation ability, dwarfing, resistance to biotic and abiotic stress, superior tree anchorage, yield, and fruit quality, as well as reduced suckering and burr knot development (Fischer 2007). A wide range of interspecific crosses have been made, and seven new *Pyrus* rootstocks have been selected, ranging from 'very dwarfing' to 'medium strong'. One of these selections, 'Pi-BU 3', has been reported to confer vigor that is 40–60% of that of *P. betulaefolia* seedling rootstocks (Elkins et al. 2012). Tree losses have been reported in German trials which may indicate that some levels of graft incompatibility must have occurred, and 'Pi-Bu 3' has not matched quince rootstocks for yield or yield efficiency (Brewer and Palmer 2011).

4.6.2.3 *P. nivalis*

Used as a rootstock, perry pear (*P. nivalis*) displays satisfactory tree anchorage, good graft compatibility, limited root suckering, adequate adaption to winter cold temperatures, and high tolerance to pear decline, but only moderate yield precocity and performance, as well as moderate tolerance to bacterial canker (Lombard and Westwood 1987). The Brossier series, developed in France in 1962, have utilized five open-pollinated seedling populations of *P. nivalis* to generate selections having a range of rootstock vigor. Furthermore, seedlings have displayed good graft compatibility, low vigor, and a range of tolerance to fire blight; however, they have also displayed poor to very poor ability for clonal propagation, ranging from 1 to 54% for semi-hardwood cuttings. The best genotype selected in this series, G28-120, confers similar tree vigor to that of 'BA29', it is graft compatible with 'Bartlett,' induces regular cropping and good fruit size, but it is susceptible to fire blight, has low ability for clonal propagation (31% by hardwood cuttings), and does not transplant well (Simard et al. 2004).

4.6.2.4 *P. calleryana*

As a seedling rootstock, *P. calleryana* exhibits very good tree anchorage and graft compatibility, moderate yield efficiency and precocity, moderate susceptibility to fruit cork spot, and resistance to black end of fruit (a physiological disorder of fruit). Grafted trees on this rootstock display high tolerance to various diseases and pests, including fire blight, *Podosphaera leucotricha* Salm. (inciting powdery mildew), *Agrobacterium tumefaciens* Conn. (inciting crown gall), *Phytophthora cactorum* Schroet (causing collar rot), *Eriosoma Pyricola* (woolly pear aphid), and *Pratylenchus vulnus* (root lesion nematode) (Lombard and Westwood 1987). Overall, *P. calleryana* has a superior adaption to most environmental conditions compared with that of *P. pyrifolia,* but it is susceptible to lime-induced chlorosis, and it is only moderately tolerant to pear decline (Tamura 2012; Teng 2011; Bell 1991).

Rootstocks of *P. calleryana* are commonly grown as seedlings in Japan, and in both North and South China. Studies have been conducted to

identify and propagate superior strains using clonal propagation (Teng 2011; Tamura 2012; Banno et al. 1988). Some strains display good rooting ability as softwood cuttings, while others exhibit growth control of grafted scion cultivars (Brewer and Palmer 2011) with marked dwarfing when grafted with Japanese cultivars (Tamura 2012). A particular clone, *P. calleryana* D6, is considered to be superior in Australia, where it is the most commonly used pear rootstock. D6 is a clonal stock selected from seed supplied by Nanjing University (China) in 1929. The rootstock is vigorous, producing a large tree when used for grafting scions, but it is compatible with most cultivars (Anon. 2014). Currently, clonal reselection rather than breeding is being conducted. Therefore, additional research efforts are required before a reliable dwarfing *P. calleryana* rootstock is developed.

4.6.2.5 *P. betulaefolia*

Rootstocks of *P. betulaefolia* have very good soil anchorage and graft compatibility, produce vigorous trees with moderate precocity and yield efficiency in scions, along with fruit that does not display black end, but with low tolerance to cork spot. *P. betulaefolia* has high tolerance to pear decline, bacterial canker, leaf spot, powdery mildew, crown gall, collar rot, woolly aphid, and root lesion nematode (Lombard and Westwood 1987). Similar to *P. calleryana*, it exhibits superior adaption to various environmental conditions, especially to hot humid conditions, and it is used widely throughout Asia (Tamura 2012). In the USA, *P. betulaefolia is* used as a rootstock on heavy clay soils and used as a standard for high vigor (Elkins et al. 2012). Although high vigor is a disadvantage, *P. betulaefolia* rootstocks are very drought and salt tolerant, can withstand temperatures down to −45 °C if cold hardened, but have low tolerance to alkaline soils (Tamura 2012). The use of *P. betulaefolia* rootstocks is also effective for avoiding black end in European pears or 'Yuzuhada' in Japanese pears. Similar to *P. calleryana*, some selections have displayed good rooting, as well as size control of scion cultivars (Tamura 2012).

4.6.2.6 *P. heterofolia*

At INRA, open-pollinated populations of *P. heterofolia* (closely related to *P. betulaefolia*) have been evaluated to select for agronomic traits, particularly for fire blight tolerance and ability for clonal propagation. Seedlings have also been screened for erect nursery habits, without branching, and for iron chlorosis tolerance (Simard et al. 2004). Scion growth grafted onto selection 'P2532' is similar to that on Quince 'BA29', but 'P2532' induces more vigorous growth of scions, similar to that of 'Old Home' × 'Farmingdale 333', and produces fruit of good size, but it is susceptible to fire blight (Simard et al. 2004).

4.6.2.7 *P. xerophila*

Rootstocks of *P. xerophila* may serve as good options in semi-arid regions, as this species is very drought tolerant. The cultivar 'Mu-Li' has displayed superior root growth in highly alkaline soils and can sustain growth in soils up to pH 8.0 (Tamura 2012).

4.6.2.8 *P. pyrifolia* Nakai

Although *P. pyrifolia* has been used as a rootstock in southern areas of China, it is not the rootstock of choice in most countries. It is not cold hardy, can be damaged under conditions of low temperatures (Yu-Lin 1996), displays poor tolerance to drought, but with flood and salt tolerance, yet it grows poorly on alkaline soils, it is susceptible to pear decline, and adapts poorly to clay soils (Bell 1991; Tamura 2012; Elkins et al. 2012). It does not produce root suckers, exhibits good tree anchorage, graft compatibility, good yield efficiency, shows moderate precocity, and has moderate tolerance to fire blight, bacterial canker, and powdery mildew, but can induce black end of in the scion (Lombard and Westwood 1987).

4.6.2.9 *P. ussuriensis* Maxim

Rootstocks of *P. ussuriensis* are the most cold hardy of the *Pyrus* species (down to −50 °C) (Teng 2011) and deemed most suitable for North Eastern China (Yu-Lin 1996). Seedlings have a

low tendency to produce root suckers, although trees have good soil root anchorage, graft compatibility, good yield efficiency, but fruit of scions is susceptible to black end. Furthermore, *P. ussuriensis* is susceptible to pear decline and root lesion nematode, but it is highly tolerant to fire blight, powdery mildew, and woolly aphid (Elkins et al. 2012; Lombard and Westwood 1987).

4.6.2.10 *P. pashia*

Nepal pear (*P. pashia*) is commonly used as a rootstock for Japanese pears in East Asia (Tamura 2012). It is also used as a rootstock in the Yunnan province of China (Yu-Lin 1996). In China, there are wide variations in morphology and vigor within seedling populations, thus providing opportunities for selecting dwarfing types (Teng 2011). *P. pashia* is not cold tolerant, and stems can be damaged at temperatures of −16 °C and below. This species tolerates low pH soils, but not high pH, and can grow on either sandy or clay soils (Bell 1991). Trees have good root anchorage and graft compatibility, but confer only moderate precocity and yield efficiency. *P. Pashia* has high tolerance to pear decline and bacterial canker, moderate tolerance to powdery mildew, collar rot, and woolly aphid, but low tolerance to fire blight, leaf spot, and root lesion nematode (Lombard and Westwood 1987).

4.6.3 *Amelanchier* Species

Dwarfing rootstocks for pear have been selected from *Amelanchier* seedlings at the Bavarian Centre of Pomology and Fruit Breeding in Germany (Brewer and Palmer 2011). This species is considered to possess moderate to high tolerance to fire blight, excellent cold hardiness, fair to good graft compatibility with *Pyrus* (high for 'Comice' and 'Beurré Hardy'), low production of root suckers, and it is potentially a non-host for pear decline, but trees can have poor root anchorage (Einhorn et al. 2017; Lombard and Westwood 1987).

Most evaluated selections offer a higher yield efficiency than 'Pyrodwarf'®, and many are either equivalent to or better than QA, and have either equal or significantly higher levels of cold hardiness than commercial *P. communis* rootstocks. Some selections look very promising as dwarfing rootstock options for US growers (Einhorn et al. 2017).

4.6.4 *Sorbus* Species

Sorbus (mountain ash) is being assessed as a potential pear rootstock that can provide scion dwarfing for intensive production. Although scion dwarfing of less than 40% of the size of *P. betulaefolia* seedling rootstocks has been reported, graft compatibility with *Pyrus* is considered poor to good (Elkins et al. 2012). The dwarfing ability of *Sorbus* along with its high tolerance to several pests and diseases are its best attributes as these trees have only moderate anchorage to the soil, and grafted scions exhibit low precocity and yield efficiency (Lombard and Westwood 1987).

4.6.5 Interspecific and Intergeneric Hybrids

Researchers at INRA have used the best selections from several different species to develop rootstocks adapted to Northern European conditions, and that are dwarfing, tolerant to fire blight, exhibit good productivity, and are easily propagated (Simard et al. 2004). Interspecific hybrids have also been used in collaboration with IRTA in Spain to develop rootstocks adapted to Mediterranean conditions. Crosses between 'Pyriam' (*P. communis*) and four Mediterranean species have been used to combine additional necessary traits of iron tolerance, drought tolerance, and propagation ability (Simard et al. 2004).

Materials of *Pyronia* (*Pyrus* × *Cydonia*) and *Sorbopyrus* (*P. communis* × *Sorbus*) are at early stages of evaluation as potential pear rootstocks. *Pyronia* is considered to have good graft compatibility with pear cultivars (Elkins et al. 2012).

In summary, various *Pyrus* and non-*Pyrus* germplasm are being used as pear rootstocks around the world. However, there have been little focused breeding efforts using this wide germplasm over a sustained period to develop rootstocks that fulfill the requirements of a modern pear orchard. A better understanding is needed of the genetics of important rootstock traits, including dwarfing, precocity, compatibility, and adaptation to a range of abiotic and biotic stresses. This is in stark contrast to our more sophisticated genetic knowledge of many of the fruit and tree characters of the scion itself.

4.7 Genomics-Assisted Breeding

Compared with other rosaceous fruit crop species, genomics-assisted breeding in pear is still in its infancy. Over the last 20 years, new genomic tools have been developed and applied to improve the efficiency and effectiveness of breeding in apple, peach, strawberry, and sweet cherry (Peace 2017; Laurens et al. 2018; van Nocker and Gardiner 2014). Applications range from a better understanding of trait genetics, through confirmation of parentage and pedigree, calculation of relatedness among potential parents, to either single-locus (MAS) or whole-genome-wide marker-assisted (genomic selection [GS]) seedling and parental selection.

The development of genomic resources specific to pear is now progressing quickly and will enable genomic-assisted breeding to proceed. The recently published draft genomes of the Chinese pear 'Dangshansuli' (Wu et al. 2013) and European pear 'Bartlett' (Chagne et al. 2014) have facilitated development of new and lower cost genotyping methods, such as GBS, to produce high-density molecular markers on pear genetic maps (Kumar et al. 2017).

As we have described, the genetics of self-compatibility, scab resistance, and harvest time have been reasonably well studied in Japanese pear, with each controlled by either one or two major genes, or by major-effect QTLs. Markers linked to these traits are being used for MAS in Japanese pear breeding (Saito 2016), thereby reducing progeny size and cost of growing seedlings to maturity in the field (Luby and Shaw 2001). However, for nearly all other selection traits that are important in pear, relationships between phenotype and genotype are less clear. Knowledge is lacking as to how many loci, and which loci, are important in consistently explaining genetic variations observed in specific traits. Further linkage analyses using biparental genetic mapping families and GWAS across less-related individuals in pear breeding germplasm sets of interest will be required to determine these large-effect marker–trait relationships, and how MAS might be best implemented in particular pear breeding programs.

GS offers the potential of utilizing large numbers of molecular markers distributed across the genome, some of which may be linked to small-, as well as to large-effect loci to explain and predict genetic variations in either one or more traits simultaneously, and without necessarily understanding the function(s) of causative loci involved (Kumar et al. 2012; Desta and Ortiz 2014). The advantage of this in fruit tree species, such as that of pear with a 4- to 10-year juvenile period, is that selections can be evaluated as potential cultivars or as breeding parents well prior to fruiting. This can significantly reduce the time frame from crossing to commercial cultivar release and increase the genetic gain per unit time.

In Japanese pear, GS has been conducted using only 162 genome-wide molecular markers in a set of 76 cultivars for nine traits having reasonably high linkage disequilibrium (Iwata et al. 2013a). These predictions have showed mostly moderate correlations with observed values (using leave-one-out cross-validations), indicating the potential of GS technology for use in this breeding germplasm, despite of the relatively low number of markers utilized. Furthermore, it has been demonstrated that GS can also predict segregation of traits in a Japanese pear progeny with reasonable accuracy, based on the whole-genome molecular marker profile of the two parents (Iwata et al. 2013b). Further studies exploring the potential uses of GS in pear breeding are warranted.

In many parts of the world, the genetic makeup of pear fruit available to consumers has not changed over the last 100 years. Efforts to develop enhanced rootstocks for pear have advanced only slightly, and pear production is often limited by the relatively poor performance of the rootstock of choice, particularly when compared with the status for apple. This provides enormous market opportunities for pear breeders to provide novel types of pear fruit and new rootstocks, by taking advantage of the wide and relatively untapped diversity among *Pyrus,* and across other genera for developing new rootstocks.

The biology of pear, as of many perennial tree fruit crops, dictates that classical breeding, which relies solely on phenotype and pedigree to produce new cultivars, will be a relatively slow and costly process in today's world. With appropriate research and cost–benefit analyses, new genomic technologies offer a potential to substantially improve pear scion and rootstock breeding efforts, thereby accelerating development of a range of new pear cultivars that will excite the future consumer, and that can be profitably grown by producers.

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