Compendium of Plant Genomes
Series Editor: Chittaranjan Kole

Schuyler S. Korban *Editor*

The Pear Genome

Springer

Compendium of Plant Genomes

Series Editor

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Whole-genome sequencing is at the cutting edge of life sciences in the new millennium. Since the first genome sequencing of the model plant Arabidopsis thaliana in 2000, whole genomes of about 100 plant species have been sequenced and genome sequences of several other plants are in the pipeline. Research publications on these genome initiatives are scattered on dedicated web sites and in journals with all too brief descriptions. The individual volumes elucidate the background history of the national and international genome initiatives; public and private partners involved; strategies and genomic resources and tools utilized; enumeration on the sequences and their assembly; repetitive sequences; gene annotation and genome duplication. In addition, synteny with other sequences, comparison of gene families and most importantly potential of the genome sequence information for gene pool characterization and genetic improvement of crop plants are described.

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The Pear Genome

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This book series is dedicated to my wife Phullara,
and our children Sourav, and Devleena

Chittaranjan Kole

Preface to the Series

Genome sequencing has emerged as the leading discipline in the plant sciences coinciding with the start of the new century. For much of the twentieth century, plant geneticists were only successful in delineating putative chromosomal location, function, and changes in genes indirectly through the use of a number of "markers" physically linked to them. These included visible or morphological, cytological, protein, and molecular or DNA markers. Among them, the first DNA marker, the RFLPs, introduced a revolutionary change in plant genetics and breeding in the mid-1980s, mainly because of their infinite number and thus potential to cover maximum chromosomal regions, phenotypic neutrality, absence of epistasis, and codominant nature. An array of other hybridization-based markers, PCR-based markers, and markers based on both facilitated construction of genetic linkage maps, mapping of genes controlling simply inherited traits, and even gene clusters (QTLs) controlling polygenic traits in a large number of model and crop plants. During this period, a number of new mapping populations beyond F_2 were utilized and a number of computer programs were developed for map construction, mapping of genes, and for mapping of polygenic clusters or QTLs. Molecular markers were also used in the studies of evolution and phylogenetic relationship, genetic diversity, DNA fingerprinting, and map-based cloning. Markers tightly linked to the genes were used in crop improvement employing the so-called marker-assisted selection. These strategies of molecular genetic mapping and molecular breeding made a spectacular impact during the last one and a half decades of the twentieth century. But still, they remained "indirect" approaches for elucidation and utilization of plant genomes since much of the chromosomes remained unknown and the complete chemical depiction of them was yet to be unraveled.

Physical mapping of genomes was the obvious consequence that facilitated the development of the "genomic resources" including BAC and YAC libraries to develop physical maps in some plant genomes. Subsequently, integrated genetic–physical maps were also developed in many plants. This led to the concept of structural genomics. Later on, the emphasis was laid on EST and transcriptome analysis to decipher the function of the active gene sequences leading to another concept defined as functional genomics. The advent of techniques of bacteriophage gene and DNA sequencing in the 1970s was extended to facilitate sequencing of these genomic resources in the last decade of the twentieth century.

As expected, sequencing of chromosomal regions would have led to too much data to store, characterize, and utilize with the-then available computer software could handle. But the development of information technology made the life of biologists easier by leading to a swift and sweet marriage of biology and informatics, and a new subject was born—bioinformatics.

Thus, the evolution of the concepts, strategies, and tools of sequencing and bioinformatics reinforced the subject of genomics—structural and functional. Today, genome sequencing has travelled much beyond biology and involves biophysics, biochemistry, and bioinformatics!

Thanks to the efforts of both public and private agencies, genome sequencing strategies are evolving very fast, leading to cheaper, quicker, and automated techniques right from clone-by-clone and whole-genome shotgun approaches to a succession of second-generation sequencing methods. The development of software of different generations facilitated this genome sequencing. At the same time, newer concepts and strategies were emerging to handle sequencing of the complex genomes, particularly the polyploids.

It became a reality to chemically—and so directly—define plant genomes, popularly called whole-genome sequencing or simply genome sequencing.

The history of plant genome sequencing will always cite the sequencing of the genome of the model plant Arabidopsis thaliana in 2000 that was followed by sequencing the genome of the crop and model plant rice in 2002. Since then, the number of sequenced genomes of higher plants has been increasing exponentially, mainly due to the development of cheaper and quicker genomic techniques and, most importantly, the development of collaborative platforms such as national and international consortia involving partners from public and/or private agencies.

As I write this preface for the first volume of the new series “Compendium of Plant Genomes,” a net search tells me that complete or nearly complete whole-genome sequencing of 45 crop plants, 8 crop and model plants, 8 model plants, 15 crop progenitors and relatives, and 3 basal plants is accomplished, the majority of which are in the public domain. This means that we nowadays know many of our model and crop plants chemically, i.e., directly, and we may depict them and utilize them precisely better than ever. Genome sequencing has covered all groups of crop plants. Hence, information on the precise depiction of plant genomes and the scope of their utilization are growing rapidly every day. However, the information is scattered in research articles and review papers in journals and dedicated Web pages of the consortia and databases. There is no compilation of plant genomes and the opportunity of using the information in sequence-assisted breeding or further genomic studies. This is the underlying rationale for starting this book series, with each volume dedicated to a particular plant.

Plant genome science has emerged as an important subject in academia, and the present compendium of plant genomes will be highly useful to both students and teaching faculties. Most importantly, research scientists involved in genomics research will have access to systematic deliberations on the plant genomes of their interest. Elucidation of plant genomes is of interest not only for the geneticists and breeders, but also for practitioners of an array of plant science disciplines, such as taxonomy, evolution, cytology, physiology, pathology, entomology, nematology, crop production, biochemistry, and obviously bioinformatics. It must be mentioned that information regarding each plant genome is ever-growing. The contents of the volumes of this compendium are, therefore, focusing on the basic aspects of the genomes and their utility. They include information on the academic and/or economic importance of the plants, description of their genomes from a molecular genetic and cytogenetic point of view, and the genomic resources developed. Detailed deliberations focus on the background history of the national and international genome initiatives, public and private partners involved, strategies and genomic resources and tools utilized, enumeration on the sequences and their assembly, repetitive sequences, gene annotation, and genome duplication. In addition, synteny with other sequences, comparison of gene families, and, most importantly, the potential of the genome sequence information for gene pool characterization through genotyping by sequencing (GBS) and genetic improvement of crop plants have been described. As expected, there is a lot of variation of these topics in the volumes based on the information available on the crop, model, or reference plants.

I must confess that as the series editor, it has been a daunting task for me to work on such a huge and broad knowledge base that spans so many diverse plant species. However, pioneering scientists with a lifetime experience and expertise on the particular crops did excellent jobs editing the respective volumes. I myself have been a small science worker on plant genomes since the mid-1980s and that provided me the opportunity to personally know several stalwarts of plant genomics from all over the globe. Most, if not all, of the volume editors are my longtime friends and colleagues. It has been highly comfortable and enriching for me to work with them on this book series. To be honest, while working on this series, I have been and will remain a student first, a science worker second, and a series editor last. And I must express my gratitude to the volume editors and the chapter authors for providing me the opportunity to work with them on this compendium.

I also wish to mention here my thanks and gratitude to the Springer staff, Dr. Christina Eckey and Dr. Jutta Lindenborn in particular, for all their constant and cordial support right from the inception of the idea.

I always had to set aside additional hours to edit books beside my professional and personal commitments—hours I could and should have given to my wife, Phullara, and our kids, Sourav, and Devleena. I must mention that they not only allowed me the freedom to take away those hours from them but also offered their support in the editing job itself. I am really not sure whether my dedication of this compendium to them will suffice to do justice to their sacrifices for the interest of science and the science community.

Kalyani, India Chittaranjan Kole

Preface

The pear, belonging to the *Pyrus* genus and subtribe Malinae of the Amygdaloideae subfamily within Rosaceae, is the third most important temperate fruit tree crop, with an annual worldwide production of ~18 million tons (2014 FAOSTAT). The genus *Pyrus* includes at least 22 known species with over 5000 accessions maintained worldwide. These accessions display wide variations in morphological and physiological traits along with broad adaptation to wide agroecological environments. It is reported that the ancient *Pyrus* likely arose during the Tertiary period, between 55 and 65 million years ago (Mya), in the mountainous regions of southwestern China. From there, it has been dispersed across mountainous ranges, both toward east and west regions, resulting in the evolution of two distinct major groups, commonly referred to as European and Asian pears. Asian pears have been cultivated for about 3300 years ago, while European pears have been cultivated for more than 2000 years.

While the cultivated European pears predominantly belong to *P. communis*, the cultivated Asian pears belong to several major species, including *P. pyrifolia*, *P.* × *bretschneideri*, *P.* × *sinkiangensis*, and *P. ussuriensis*. Fruit of European pears is characterized by their typical pyriform shape (bulbous bottoms and tapering tops), although there are some with oblate or globose shapes, with soft and fine-grained flesh, few stone or lignified cells, along with a strong aroma and flavor. Fruit of Asian pears is predominantly round in shape, although there are some with pyriform shapes, firm, with a crispy flesh, high sugar, and low acid contents, along with faint aroma and mild flavor.

The pear tree is cross-pollinated, self-incompatible, and with a long juvenility period of 5–7 years. However, there are little barriers to interspecific hybridization in pear despite its wide geographic distribution. Although genetic studies are limited, it is well documented that there is a wide genetic variability in pear. Most commercially grown cultivars have been selected as chance seedlings and then subsequently maintained through vegetative propagation, although there are few cultivars that have been developed from breeding programs via sexual hybridization. There are few releases of new pear cultivars that have been derived from various breeding programs from around the world. As with other tree fruit breeding programs, classical pear breeding is a long-term and expensive effort. Thus, recent advances in pear genomics are paving the way for a new and promising path for pear genetic improvement initiatives and efforts.

In recent years, modern genetic and genomic tools have resulted in the development of a wide variety of valuable resources, including molecular markers, genetic mapping, genetic transformation, structural and functional genomics resources, genome sequencing, and genome-wide association studies, as well as comparative genomic studies. These tools and resources offer unparalleled opportunities to pursue genetic improvement efforts to combine fruit quality, high productivity, precocious fruit-bearing, long postharvest storage life, along with elevated levels of resistance to various major diseases and insect pests of pear. Furthermore, these new genetic tools and genomic resources provide unprecedented opportunities to explore and understand genetic variation, evolution, and domestication of pear, as well as to better establish population-level relationships among different pear species. In the past few years, completion of whole-genome assemblies of “Dangshansuli”, an Asian pear, and “Bartlett”, a European pear, has enabled new discoveries in pear, including those of genomic structure, chromosome evolution, and patterns of genetic variation. All this wealth of new resources will have a major impact on our knowledge of the pear genome and its expanding resources. In turn, these resources and knowledge will have significant impacts on efforts for genetic improvement of pears.

The Pear Genome book will cover our current knowledge of botanical and taxonomic classifications; origin, distribution, and early documented distribution of pear; germplasm resources; genetic studies and genetic improvement efforts; genetic linkage maps; molecular genetic and QTL analysis, along with genomic analysis; whole-genome sequencing strategies and outcomes; repetitive and regulatory sequences; self-incompatibility; stone cell development; vegetative budbreak analysis; fire blight genetics and genomics; functional genomic analysis; whole-genome duplication in pear and its comparisons to apple; and potential opportunities and challenges for future genetic improvement efforts of pears.

All 16 chapters included in this volume will provide a wealth of information and comprehensive overview of the status of early and ongoing efforts to discern the genetics, breeding, and genomics of the pear. This book will offer ideas, opportunities, and pathways that will support future research and discovery efforts that will not only contribute to our expanded knowledge of various traits of this important fruit crop, as well as our understanding of the pear genome as a whole, but these will also contribute to overall advances in genetic enhancement efforts of the pear.

Urbana, USA Schuyler S. Korban

Contents

Abbreviations

4CL	4-coumarate: coenzyme A ligase
AFLP(s)	Amplified fragment length polymorphism(s)
CAD	Cinnamyl alcohol dehydrogenase
CCR	Cinnamoyl-CoA reductase
CR(s)	Chilling requirement(s)
CRISPR/cas9	Clusters of regularly interspaced short palindromic repeats/cas9 associated protein
CU(s)	Chilling unit(s)
DIR	Dirigent
G × E	Genotype × environment
GE	Genetic engineering
GMO	Genetically modified organism
GRF	Growth-regulating factor
GS	Genomic selection
GSI	Gametophytic self-incompatibility
GWAS	Genome-wide association study(ies)
HCT	Hydroxycinnamoyl-CoA: shikimate/quinate hydroxycinnamoyltransferase
HSF(s)	Heat shock transcription factor(s)
IRAP	Inter-retrotransposon amplified polymorphism
LD	Linkage disequilibrium
LG(s)	Linkage group(s)
LM	Linkage mapping
MAB	Marker-assisted breeding
MAS	Marker-assisted selection
NGS	New gene sequencing
NPBT	New plant breeding techniques
OA	Organic agriculture
OMT	O-methyltransferase
POD	Peroxidase
QTL(s)	Quantitative trait locus/loci
RAPD(s)	Random amplified fragment length polymorphism(s)
RBIP	Retrotransposon-based insertion polymorphism
RNAi	RNA interference
SBP	SQUAMOSA promoter binding protein

SI	Self-incompatibility
siRNAs	Small interfering RNAs
SNP(s)	Single nucleotide polymorphism(s)
SSAP	Sequence-specific amplification polymorphism
SSN	Sequence-specific nuclease technology
SSR(s)	Simple sequence repeat(s)
TE(s)	Transposon(s)/able element(s)
TF(s)	Transcription(al) factor(s)
VB	Vegetative budbreak
VIGS	Virus-induced gene silencing
WGD(s)	Whole-genome duplication(s)
ZHD	Zinc finger homeodomain

1 Botany and Taxonomy of Pear

Muriel Quinet and Jean-Pierre Wesel

Abstract

Pear belongs to the Rosaceae family as most of the cultivated fruit trees. It is the second fruit tree crop in terms of production after apple. Its production has increased these last decades to reach a world production of more than 27 megatons for almost 1,600,000 ha. Pears have been cultivated in Europe and in Asia for more than 5000 years. Of all known and reported pear species and interspecific hybrids, five are mainly cultivated. These include the European pear, *Pyrus communis*, and the Asian pears *P. pyrifolia*, *P.* × *bretschneideri*, *P. ussuriensis*, and *P. sinkiangensis*. Fruits of European pears are elongated and have a full-bodied texture, while those of Asian pears are round and have a sandy texture. The *Pyrus* genus belongs to the Amygdaloideae subfamily and the Malinae tribe and consists of about 75–80 species and interspecific hybrid species. As several hybridizations are observed among *Pyrus* species, this renders the distinction among some pear species rather difficult. The origin of the *Pyrus* genus dates back to the Oligocene epoch, about 33.35–25.23 Mya. It is a genus of mainly deciduous trees and shrubs spread throughout temperate Eurasia, reaching the Atlas Mountains in North Africa and extending to Japan and South China. *Pyrus* species produce generally simple leaves alternately arranged. Leaves are glossy green on some species, densely silvery hairy in some others. *Pyrus* flowers are white, borne in corymbs on short spurs or lateral branchlets and are composed of five sepals, five petals, numerous stamens, and usually a five-locular ovary with free styles. The *Pyrus* fruit is a pseudo-fruit composed of the receptacle or the calyx tube, greatly dilated, enclosing the true fruit, and consisting of five cartilaginous carpels, known as the core. Morphological characters of the leaf, fruit, and calyx are commonly used to differentiate among *Pyrus* species. There are thousands of pear cultivars over the world with wide diversity for fruit shape, taste, and texture. In this chapter, we have focused on the description of cultivated *Pyrus* species and on some of the main cultivated cultivars.

1.1 Introduction

Two of the main pear species that are cultivated include *Pyrus communis* L. and *P. pyrifolia* (Burm.f.) Nakai (Hedrick et al. 1921). *P. communis* is native to central and Eastern

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Europe and to southwest Asia, and it is known as European pear or common pear. It is one of the most important fruits of temperate regions, and it is the pear of common cultivation in Europe, America, Oceania, and Africa (Hedrick et al. 1921; Bassil and Postman 2010). The cultivation of *P. communis* makes up about one-third of the total pear production (Chagné et al. 2014). While *P. pyrifolia* is native to East Asia, and it is mainly cultivated in Asia, it is currently also cultivated in America, Oceania, and Europe (Bretaudeau and Fauré 1991; White 2002; Faoro and Orth 2014). Other *Pyrus* species are also commonly grown in Asia, including *P.* × *bretschneideri*, *P. ussuriensis,* and *P. sinkiangensis* (Wu et al. 2013). *P. pyrifolia* is known by many names including Asian pear, Chinese pear, Korean pear, Japanese pear, Taiwanese pear, nashi, and sand pear (Hedrick et al. 1921; Bailey and Bailey 1976; Petri and Herter 2002; Lee et al. 2012). Some of these vernacular names include other pear species, as some cultivars of *P.* × *bretschneideri* and *P. ussuriensis* are also called nashi pears, or *P.* × *bretschneideri* is also known as Chinese white pear (Chagné et al. 2014). For the sake of clarity, all these will be collectively grouped and referred to as Asian pears. While fruits of European pears are elongated and have full-bodied textures, fruits of Asian pears are round and have sandy textures (Silva et al. 2014). All these *Pyrus* species are botanically referred to as pome fruits and belong to the Rosaceae family, as many other fruit tree species including other pome fruits, apple and quince, and stone fruits, such as cherry, almond, peach, apricot, plum, and nectarine.

The first landmarks of pear as a cultivated tree in Europe were found in ancient Greece (Hedrick et al. 1921). Pear is currently cultivated worldwide, and its production has increased over the last decades to reach a world production of more than 27 megatons for almost 1,600,000 ha in 2016 (Fig. 1.1a, b) (FAO 2018). China is the largest producer of pear fruits worldwide, producing about 20 times more pears than all other main producers (Fig. 1.1c) (FAO 2018). In 2016, Asia contributed for 79% of pear production, Europe for 10%, America for 7%, Africa for 3%, and Oceania for less than 1% (FAO 2018). The pear tree is the second Rosaceous fruit tree crop grown in terms of production and the fifth in terms of harvested area (Fig. 1.2). Overall, the main cultivated fruit tree is apple, and pear production is about 30% of apple production. Pear and apple yields average 168,000 hg/ha over the last years, and are the best yields among Rosaceous fruit trees (FAO 2018).

1.2 Origin and Cultivation of Pear

1.2.1 Origin of Pear

The exact origin of the cultivated European pear tree is not known (Hedrick et al. 1921). According to Debuigne and Couplan (2006), it may result from the hybridization of several wild pear species from Europe and Minor Asia, including *P. communis* subsp. *pyraster* (L.) Ehrh. The wild pear tree of *P. communis* subsp. *pyraster* has likely originated from the mountains of Minor Asia or from Europe (Opoix 1896; Pesson and Louveaux 1984; Paris 1996). It could be deemed as a relic of warm oak forests and would be indigenous of the medio-European flora (Aas 1999). It most probably migrated to central and Western Europe 7500 to 4500 years ago during the warm post-glacial period (Aas 1999). The natural range of the species has not been precisely identified as it is difficult to distinguish wild from cultivated *P. communis* (Aas 1999). Currently, the species could be found in large areas of temperate regions of Europe, Asia, and America at altitudes of up to 800 m (Pesson and Louveaux 1984).

In contrast, domestication of Asian pears, including their centre(s) of origin along with time periods, is clearly documented (Silva et al. 2014). As reported in written Chinese (Shijing) and in other books, the major Asian species, cultivated for at least 1500 years, are *P. pyrifolia* and *P. ussuriensis* (Silva et al. 2014). In Japan, pear seeds dating back to the first century ACN have been found during excavations of the Toro Ruins in the Shizuoka prefecture (Saito 2016).

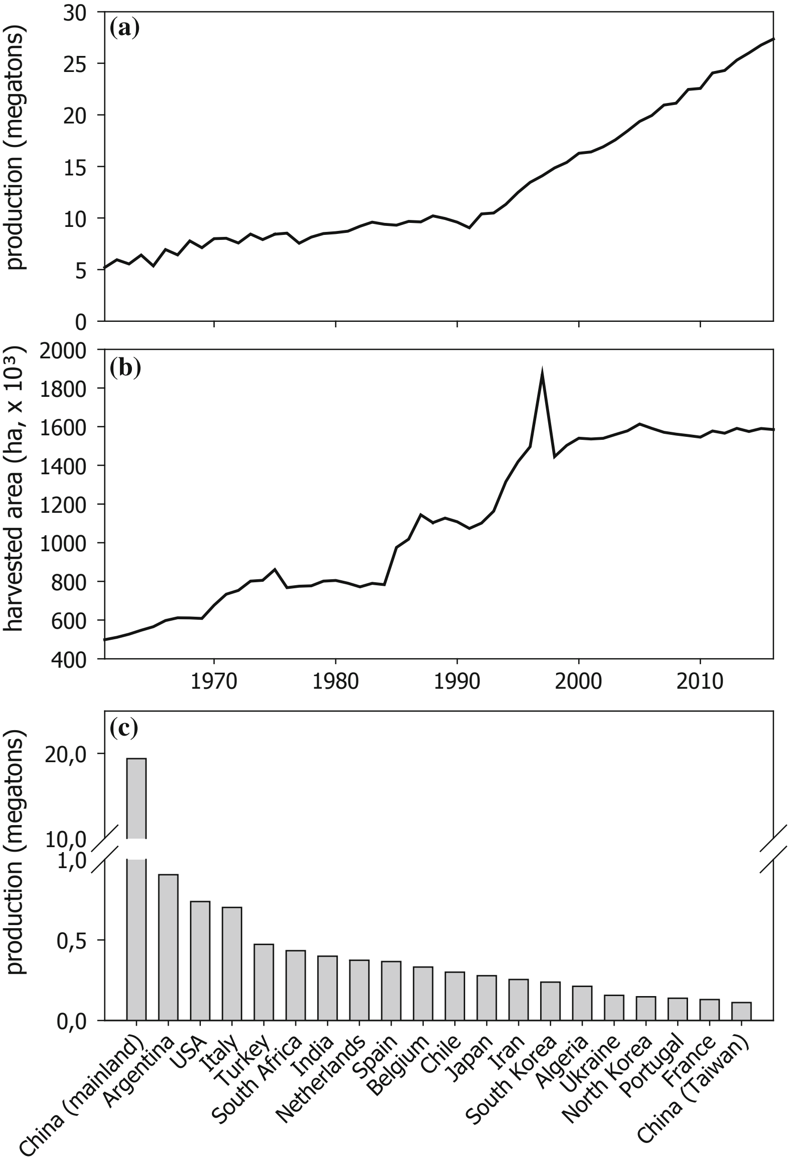

Fig. 1.1 Evolution of worldwide pear cultivation. **a** Pear production and **b** pear harvested areas between 1961 and 2016. **c** Main countries producing pears in 2016. Based on FAOSTAT database (FAO 2018)

1.2.2 History of Pear Cultivation

In comparison to other fruit tree species, pear cultivation has occurred rather late, and this is mainly due to the small fruit size of primitive pears (De Vilmorin and Clebant 1996). Pear domestication has taken place independently in the Far East (China) and in the Caucasus region (Ferradini et al. 2017). Pear has been cultivated in ancient Greece under the name of 'Achras' around 2800 ACN (Hedrick et al. 1921; Bretaudeau and Fauré 1991). By this time, pear has also been cultivated in both ancient Egypt and ancient Rome; however, its cultivation in China would have to go back to 4000 ACN (Bretaudeau and Fauré 1991).

In Homer's Odyssey is the first mention of pear cultivation in Greek literature (Royer 1853; Hedrick et al. 1921); however, the first definitive records of pear cultivation are found in the writings of Theophrastus in 370–286 ACN (Leroy 1867; Hedrick et al. 1921). Theophrastus

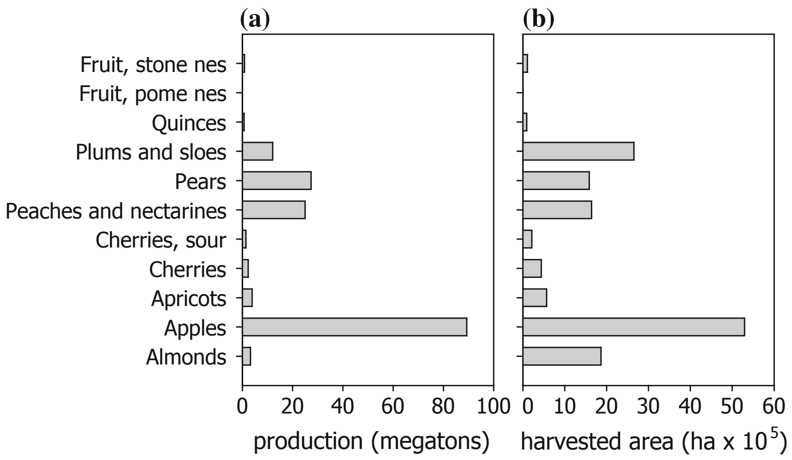

Fig. 1.2 Rosaceous fruit tree production (**a**) and harvested area (**b**) in 2016. Based on FAOSTAT database (FAO 2018)

distinguishes between wild and cultivated pears, and he makes reference to four pear cultivars, including 'Myrrha', 'Nardinon', 'Onychinon', and 'Talentiaion' (Leroy 1867; Hedrick et al. 1921). He writes about the propagation of pears from seeds, roots, and cuttings, as well as recognizes the necessity for cross-pollination though he does not offer reasons for this practice (Hedrick et al. 1921). In 178 ACN in Italy, Cato wrote the first book, written in Latin, on agriculture, and described six pear cultivars (Hedrick et al. 1921). Cato describes almost every method of propagating, grafting, caring for, and keeping fruits known to twentieth-century fruit growers (Hedrick et al. 1921). Following two centuries, Pliny described 41 pear cultivars in *Historia naturalis* (Leroy 1867). From Pliny, we know that the Romans valued pears for medicinal purposes, as well as for food (Hedrick et al. 1921). Subsequently and for a period of 1500 years, there are a few new facts that have been offered regarding the evolution of the pear (Hedrick et al. 1921). Many Roman writers mentioned pear, but they have all copied Theophrastus, Cato, and Pliny (Hedrick et al. 1921). In Japan, the first evidence of pear cultivation is found in the Chronicles of Japan (720 ACN), which mention that cultivation of fruits and nuts has been promoted during the Jito Tenno era (686–696 ACN) to fight famine (Saito 2016).

In Europe, there is no mention of new pear cultivars during the early Middle Ages, but in the eleventh century, Charlemagne has recommended planting fruit trees, including pear trees, in *Capitulare de Villis* (Leroy 1867). Therefore, the credit for establishing the first notable landmark in the history of the pear in France is due to Charlemagne (Hedrick et al. 1921). In fact, he has commanded his orchardists to plant pears of distinct kinds for distinct purposes and has cited the following three cultivars: 'Dulciores' for fresh fruit, 'Cocciore' for cooking, and 'Serotina', a late maturing variety (Leroy 1867). Following Charlemagne, there are no records on agricultural activities for the next five centuries (Hedrick et al. 1921). Undoubtedly, fruit tree farming must have been preserved in abbeys; however, there are no records of names of the pear cultivars cultivated in Western Europe during this period until the end of the fourteenth century (Leroy 1867).

During the fifteenth century, the printing press was by then developed, and books about horticulture were written and printed (Leroy 1867). The *Seminarium* of Charles Estienne, printed in 1540, offered brief descriptions of 16 pear cultivars that are still known to this day (Leroy 1867). From *Le Théâtre d'Agriculture,* written by De Serres and published in 1608, we know that many pears of diverse shapes, colours, flavours, and perfumes existed in the year 1600 in France

(Hedrick et al. 1921). Enthusiasm for pears rapidly increased due to the interest of a French royal prosecutor, Le Lectier (Leroy 1867). Le Lectier collected all available fruits of his time and in his country (Hedrick et al. 1921). In *Catalogue des arbres cultivés* published in 1628, he classified 260 pear cultivars based on their maturation. The French King Louis XIV (1638–1715) promoted pear cultivation, and during his reign, new cultivars were developed (Leroy 1867). Hitherto, the development of new cultivars was done through picking and transplantation of trees encountered in nature or in cultivated gardens. Although it has been a common practice since ancient Rome, cultivar selection of *P. communis* was mainly developed during the eighteenth century in Europe (Pesson and Louveaux 1984). In Japan, the concept of cultivars and cultural techniques were developed during the middle of the Edo era (1603–1867). 'Shokokusanbutsuchou' was the first recorded Japanese pear cultivar in 1735, and it was mentioned along with over 100 pear cultivars (Saito 2016).

During the eighteenth century in Europe, knowledge and understanding of plant sexuality have prompted the pursuit of plant breeding (Leroy 1867). Growers have made crosses and sowed seeds in order to develop new cultivars (Table 1.1) with improved pear fruit flavour, texture, size, and colour (Hedrick et al. 1921). Most of these new cultivars have been developed in Belgium, and several of these cultivars are cultivated to this day (Leroy 1867).

Pear improvement efforts in Belgium within a single century surpass all other previous efforts (Hedrick et al. 1921). Belgian pear growers and well-suited soil and climate conditions must be given credit for the development of the modern pear (Hedrick et al. 1921). The first and most famous Belgian to sow pear seeds in order to obtain new cultivars was Abbot Nicolas Hardenpont (1705–1774), and a dozen or more new pears have been credited to him (Hedrick et al. 1921). Hardenpont's best cultivars have been known since 1758, including the popular 'Passe-Colmar' (1758), 'Beurré d'Hardenpont' (1759), 'Délice d'Hardenpont', 'Beurré Rance', and 'Délice du Panisel' (1760–62). 'Beurré d'Harpendont' could still be found in tree nurseries worldwide, although it is now known as 'Glou Morceau' in Anglo-Saxon countries and as 'Beurré d'Arenberg' in France. Jean-Baptiste Van Mons has followed Hardenpont's lead by developing about 500 new pear cultivars among thousands found in Belgium between 1758 and 1900. Among these, 'Beurré d'Anjou' (syn. 'Nec plus Meuris') has been exported to America where it is still cultivated. It is important to point out that the designation of 'Anjou' or 'd'Anjou' has been erroneously used for this variety when first introduced to both America and England. Nevertheless, almost 40 pear cultivars developed by Van Mons have remained under cultivation at the beginning of the twentieth century (Hedrick et al. 1921). In fact, it is Van Mons' work that has promoted fruit-growing in Europe and America, and pomologists are in general agreement that until his time, no man has exerted such profound influence on the field of pomology (Hedrick et al. 1921). Again, it is Belgian breeders from *Pomone tournaisienne* who have developed 160 pear cultivars, including 'Beurré de Naghin' (Wesel 1996). In the Belgian city of Mechelen, Pierre Joseph Esperen developed 70 cultivars, such as 'Bergamotte Esperen', while in another Belgian city Jodoigne, 13 breeders developed about 200 new pear cultivars (Wesel 1996). Among the latter group of cultivars, and of particular note, are 'Triomphe de Jodoigne', developed by the brothers Bouvier, 'Alexandrina', developed by Alexandre Bivort, and 'Madame Grégoire', developed by Xavier Grégoire (Wesel 1996).

As new cultivars have been developed in Belgium, similar efforts have been undertaken in France, leading to such present-day cultivars as 'Beurré-Hardy', 'Bonne Louise d'Avranches', 'Doyenné du Comice', and 'Triomphe de Vienne', in the UK, resulting in 'William's (Bon Chrétien)', 'William's Duchess', and 'Conference', and in the USA, notably 'Clapp's Favourite'. Although central and western Europe have contributed some efforts for the development of pear cultivars, somewhat similar to those efforts undertaken in Italy, France, Belgium, and

Table 1.1 Major cultivars of European pear (*Pyrus communis*) identified during the eighteenth and nineteenth centuries

Cultivar	Synonyms	Breeder(s)	Year	Country
Beurré d'Hardenpont	Beurré d'Arenbert Glou Morceau	N. Hardenpont	1759	Belgium
William's	Bartlett Bon Chrétien Williams	Stair/William	1770	UK
Légipont	Fondante de Charneux Miel de Waterloo Köstliche von Charneux	M. Légipont	1805	Belgium
Durondeau	Poire de Tongres Beurré Durondeau	Ch.-L. Durondeau	1811	Belgium
Beurré d'Anjou	Nec plus Meuris Anjou	J. B. Van Mons	1822	Belgium
Joséphine de Malines		J. Esperen	1830	Belgium
Beurré Hardy		Ernest Bonnet	1830	France
Rocha		P. A. Rocha	1836	Portugal
Doyenné du Comice	Vereinsdechants birne Decana del Comicio	Jardin du Comice	1849	France
Beurré de Naghin		N. de Naghin	1858	Belgium
Madame Grégoire		X. Grégoire	1860	Belgium
Clapp's favourite	Clapps Liebling	T. Clapp	1860	USA
Abbé Fetel	Abate Fetel	Abbé Fetel	1869	France
Triomphe de Vienne		J. Colaud alias (Côte)	1870	France
Conference		Firme Rivers	1890	UK
Packhams Triumph		C. H. Packham	1896	Australia
Forelle			>1670	Germany

England, it is Germany that is most noted for providing valuable literature in the field of pomology (Hedrick et al. 1921).

In Japan, commercial pear production has substantially increased around the same period of time as in Europe due to successive discoveries of two chance pear seedlings, 'Nijisseiki' and 'Chojuro', around the year of 1890 (Saito 2016). During the Edo period in Japan (1603–1868), over 150 cultivars have been documented (Silva et al. 2014). Whereas cultivars of European pears have come to the New World almost entirely from the countries of Belgium and France, along with three or four major cultivars of English origin that have been most commonly grown in North America in the twentieth century (Hedrick et al. 1921). Most, if not all of the cultivars that have originated in USA, until the middle of the nineteenth century, have come from imports due to French, Dutch, and English settlements (Hedrick et al. 1921). Moreover and of particular impact on the US pear industry is the introduction of oriental (Asian) pears and their hybrids (Hedrick et al. 1921). Asian pear cultivation has intensified in the USA around 1938 (Bretaudeau and Fauré 1991), and has since spread worldwide (Bretaudeau and Fauré 1991). It is reported that the oriental, Chinese, or sand pear came into America from Asia by way of Europe through the Royal Horticultural Society of London (Hedrick et al. 1921). Hybridizations with the European pear gave rise to 'Le Conte' (1846), 'Kieffer' (1873) or 'Garber' (1880) (Hedrick et al. 1921). It is important to point out that cultivation of *P. pyrifolia* dates back to 693 ACN in Japan (Bretaudeau and Fauré 1991).

During the twentieth century, private and national research stations in Europe, North America, and Asia established fruit breeding programs to develop new commercial cultivars. Overall, the number of newly developed and released cultivars of pear has been a lot less than those for apple (Brewer and Palmer 2011). Among the limited number of pear cultivar releases developed from pear breeding programs is 'Concorde', developed at East Malling (UK) in 1977 and derived from a cross between 'Conference' and 'Doyenné du Comice'. However, efforts undertaken by Japanese and Chinese breeding programs during the twentieth- and twenty-first centuries resulted in the release of various new Asian pear cultivars (Jun and Hongsheng 2002; Teng 2011; Saito 2016).

Overall, several pear breeding programs have focused their efforts on pest and disease resistance, fruit quality and appearance, duration of harvest season, self-fertility, yield, and growth habit (Jun and Hongsheng 2002; Brewer and Palmer 2011; Dondini and Sansavini 2012). It is only in the last 15–20 years that nearly 300 novel cultivars, including about 200 European pear and 100 Asian pear cultivars, have been released (Dondini and Sansavini 2012). Nowadays, there are several thousands of pear cultivars that are available worldwide. Among these, approximately ten cultivars account for 90% of the world production of pears (Pesson and Louveaux 1984; Miranda et al. 2010). However, due to cultivar history and propagation methods, some cultivars are known under different names in different regions or that different cultivars are grown/promoted as being the same; thus clearly indicating that pear cultivars are not as well characterized as previously reported (Evans et al. 2015). Therefore, genetic molecular markers are currently being used to screen accessions of different germplasm collections, and considerable efforts are needed to verify and confirm accurate identities of accessions in worldwide national collections (Evans et al. 2015).

1.3 Taxonomy and Phylogeny of Pears

1.3.1 The *Pyrus* Genus Within Rosaceae

Both European and Asian pears belong to the genus *Pyrus* of the family Rosaceae within the Order Rosales, belonging to the Rosids subclass, and within the Eudicot core (Chase et al. 2016). The Rosaceae family is monophyletic with a moderately large angiosperm lineage containing 90 genera and between 2500 and 2900 species (Stevens 2017). Rosaceae is a heterogeneous family that is divided into the following three subfamilies, according to APG IV, Dryadoideae, Rosoideae, and Amygdaloideae (Stevens 2017). Previously, largely based on fruit and other morphological characteristics, Rosaceae was divided into four subfamilies, including Rosoideae, Maloideae, Amygdaloideae, and Spiraeaoideae (Xiang et al. 2017). However, recent molecular analyses support the separation of the former Rosoideae (s.l.) into Rosoideae (s.s.) and Dryadoideae, and in combining the previous Maloideae, Amygdaloideae (s.s.), and Spiraeaoideae into the current Amygdaloideae (s.l.) (Stevens 2017; Xiang et al. 2017). The species richness of Rosaceae could be partly related to polyploidization and to species radiation in the family's history (Xiang et al. 2017). Relationships among Rosaceae tribes and genera remain unclear, in part because of polyploidy events and rapid separation/diversification among some clades (Xiang et al. 2017). Phylogenetic studies of Xiang et al. (2017) suggest that Dryadoideae is the basal clade of Rosaceae, and it is the sister of the combined clade of Rosoideae and Amygdaloideae. The age of the crown Rosaceae is about 101.6 Mya with the separation of Dryadoideae, followed by an immediate divergence of the two largest subfamilies Rosoideae and Amygdaloideae at 100.7 Mya (Xiang et al. 2017).

The subfamily Amygdaloideae contains about 1000 species (Xiang et al. 2017), and it is divided into 11 tribes, including the Malinae (Stevens 2017). All, but two of the tribes of Amygdaloideae, must have diverged between 96 and 88 Mya., with no further activity for the next 20 Mya (Xiang et al. 2017). The Malinae may represent a rapid but ancient radiation (Campbell et al. 2007; Stevens 2017; Xiang et al. 2017). This is perhaps associated with whole genome duplication in the stem lineage, and accompanied with climatic changes that must have occurred at the end of the Palaeocene and all through towards the beginning of the Oligocene (Xiang et al. 2017). The stem group Malinae is dated back to the late Palaeocene, with subsequent divergence in the Eocene and Oligocene epoques (Lo and Donoghue 2012).

Despite efforts to elucidate relationships within the Malinae, relationships among the major sublineages, generic limits, and divergence times have remained uncertain (Campbell et al. 2007; Lo and Donoghue 2012). Most probably, hybridization has played a part in the Malinae evolutionary history, as hybridization is unusually common among genera in this tribe (Campbell et al. 2007). Comparisons of genetic linkage maps within Malinae have suggested that all chromosomes of the genera in this tribe show co-linearity despite considerable differences in genome sizes (Yamamoto and Terakami 2016). The Malinae contains 1000 species organized within 30 genera (Stevens 2017). However, Malinae is also known as Cydoniaceae, Malaceae, Mespilaceae, Pyraceae, or Sorbaceae (Stevens 2017). Furthermore, Malinae is characterized by a north temperate distribution, production of leaves with deciduous stipules, flowers with a gynoecium that is at least half-way inferior, and a fleshy hypanthium ‘pome’ fruit (Stevens 2017). Several important edible fruits are members of this tribe, such as apple (*Malus*), pear (*Pyrus*), quince (*Cydonia*), loquat (*Eriobotrya*), chokeberry (*Aronia*), and serviceberry (*Amelanchier*) (Campbell et al. 2007). In addition, the Malinae tribe includes valued ornamentals, such as some cotoneasters (*Cotoneaster*), hawthorns (*Crataegus*), Japanese quinces (*Chaenomeles*), firethorns (*Pyracantha*), and mountain ashes (*Sorbus*) (Campbell et al. 2007).

1.3.2 Phylogeny of *Pyrus*

The genus *Pyrus* is characterized by a high genetic variability, and it consists of around 75 species and interspecific hybrid species, along with thousands of cultivars (Ferradini et al. 2017; Stevens 2017). Estimates of *Pyrus* diversity vary between 50 and 80 species, according to various publications (Table 1.2), and the numbers of accepted species differ as a consequence of poorly understood species limits (Korotkova et al. 2014). Indeed, up to 900 *Pyrus* species names have been recorded (Zheng et al. 2014). However, the number of primary (i.e., not of hybrid origin) species has been relatively consistent, and approximately 20 putative primary species are widely recognized (Zheng et al. 2014). Estimation of genetic diversity among *Pyrus* spp. has been difficult due to low morphological diversity, lack of differentiating characters among species, and widespread cross-ability (Yao et al. 2010). Although they are interspecies compatible, *Pyrus* species are typically self-incompatible (Yue et al. 2014).

The *Pyrus* origin dates back to the Oligocene epoque, about 33.35–25.23 Mya (Korotkova et al. 2018). It is a genus of deciduous trees and shrubs occurring throughout temperate Eurasia, reaching the Atlas Mountains in North Africa, and extending to both Japan and South China (Korotkova et al. 2018). Assessing species diversity in *Pyrus* is challenging due to high morphological plasticity and frequent hybridizations within the genus (Korotkova et al. 2018). Thus, this genus is characterized by very low genetic distances between taxa (Korotkova et al. 2014). Currently, the genus is subdivided into the following four sections: *Pyrus* sect. *Pyrus*, *Pyrus* sect. *Xeropyrenia* Fed., *Pyrus* sect. *Argyromalon* Fed., and *Pyrus* sect. *Pashia Koehne* (Korotkova et al. 2018). However, phylogenetic analyses

Table 1.2 List and origin of *Pyrus* species (Asanidze et al. 2011; Silva et al. 2014)

Species	Country or region of origin
P. alnifolia (S. and Z.) Franch. and Sav.	Russian Far East, China, Japan, Korea, Taiwan
P. americana DC	Greenland, USA, Canada
P. angustifolia Aiton	USA, Canada
P. arbutifolia (L.) L.f.	USA
P. aria (L.) Ehrh.	USA, Canary Islands, North Africa, All of Europe
P. armeniacifolia T.T. Yu	China
P. aucuparia var. dulcis (K.) A. and G.	All Europe
P. aucuparia var. randaiensis Hayata	Taiwan
P. baccata L.	Russia, Mongolia, China, Korea
P. baccata var. aurantiaca Regel	Russia, Mongolia, China, Korea
P. baccata var. himalaica Maxim.	China, Bhutan, India, Nepal
P. baccata var. mandshurica Maxim.	Russia, China, Japan, Korea
P. betulifolia Bunge	China, Laos
P. boissieriana Buhse	Azerbaijan, Turkmenistan, Iran
P. bulgarica Kuth. and Sachokia (*P.* × *nivalis* Jacq.)	Western Europe, Central Eastern and Southern
P. calleryana Decne.	China, Korea, Taiwan, Vietnam
P. calleryana var. dimorphophylla (Makino) Koidz.	Japan
P. calleryana var. fauriei (C. K. Schneid.) Rehder	Korea
P. calleryana var. koehnei (C. K. Schneid.) T. T. Yu	China
P. cathayensis Hemsl.	China
P. caucasica Fed.	Eastern Europe and Central Greece
P. chamaemespilus (L.) Ehrh.	Western Europe, Central Eastern and Southern
P. communis L.	All Europe
P. communis subsp. gharbiana (T.) Maire	Algeria, Morocco
P. communis subsp. *P. marmorensis* (Trab.) Maire	Morocco
P. communis subsp. *P. pyraster* (L.) Ehrh.	Western Europe, Central Eastern, and Southern
P. communis var. cordata (Desv.) H.f.	UK, Portugal, Spain, France
P. coronaria L.	Canada, USA
P. coronaria var. ioensis Alph. Wood	USA
P. cossonii Rehder	Algeria
P. crataegifolia Savi	Turkey, Albania, Serbia, Greece, Italy, Macedonia
P. cuneifolia Guss.	Central Eastern Europe, South and Central
P. cydonia L.	Iran, Armenia, Azerbaijan, Russia, Turkmenistan
P. decipiens Bechst.	All Europe and North Africa
P. delavayi Franch.	China

(continued)

Table 1.2 (continued)

Species	Country or region of origin
P. demetrii Kuth	Georgia
P. discolor Maxim.	China
P. diversifolia Bong.	USA, Canada
P. domestica (L.) Sm.	Algeria, Cyprus, Eastern Europe Central, West and Meridional
P. doumeri Bois	Vietnam
P. elaeagrifolia Pall.	Turkey, Ukraine, Albania, Bulgaria, Greece, Romania
P. elaeagrifolia subsp. kotschyana	Turkey
P. floribunda Lindl.	USA, Canada
P. folgner (C. K. Schneid.) Bean	China
P. foliolosa Wall.	Burma, Bhutan, India, Nepal, China
P. fusca (Raf.) C. K. Schneid.	USA, Canada
P. georgica Kuth	Georgia
P. germanica (L.) Hook. f.	Middle East, Eastern Europe, Central, Southern and Northern Asia
P. gharbiana Trab.	Morocco
P. glabra Boiss.	Iran
P. gracilis Siebold and Zucc.	Japan
P. harrowiana Balf. f. and W. W. Sm.	China, India, Nepal, Burma
P. heterophylla Regel and Schmalh.	Kyrgyzstan, Tajikistan, China
P. hondoensis Nakai and Kikuchi	Japan
P. hupehensis Pamp.	China, Taiwan
P. indica Wall.	South Asia and Far East Asia
P. intermedia Ehrh.	All Europe
P. japonica Thunb.	Japan
P. kansuensis Batalin	China
P. keissleri (C. K. Schneid.) H. Lev.	China, Myanmar
P. ketzkhovelii Kuth	Georgia
P. korshinskyi Litv.	Afghanistan, Tajikistan, Uzbekistan
P. korshinskyi Litv. subsp. bucharica (Litv.) B. K	Former Soviet Union
P. kumaoni Decne.	Middle East, Far East and South Asia
P. lanata D. Don	Afghanistan, India, Nepal, Pakistan
P. malus subsp. paradisiaca (L.)	Western, Eastern, and Central Europe and Greece
P. matsumurana Makino	Japan
P. minima Ley	UK
P. nebrodensis Guss.	Italy - Sicily
P. nussia Buch.-Ham. ex D. Don	Far East, South Asia
P. pinnatifida Ehrh.	All Europe
P. pohuashanensis Hance	Russia, China, Korea
P. praemorsa Guss	South of Italy, France
P. prattii Hemsl.	China
P. prunifolia Willd.	China

(continued)

Table 1.2 (continued)

Species	Country or region of origin
P. pseudopashia T.T. Yu	China
P. pyrifolia var. pyrifolia	China, Laos, Vietnam
P. ringo var. kaido Wenz	China
P. ringo Wenz.	China, Korea
P. sachokiana Kuth.	Georgia
P. salicifolia Pall.	Iran, Armenia, Turkey, Azeebaijan
P. sanguinea Pursh	Canada, USA
P. scabrifolia Franch.	China
P. scalaris (Koehne) Bean	China
P. sieboldii Regel	China, Japan
P. sikkimensis Hook. f.	China, Bhutan, India
P. sinensis var. maximowicziana H. Lev.	Korea
P. spectabilis Aiton	China
P. spinosa Forssk.	Central Eastern Europe, South, and Central
P. sudetica Tausch	Western Europe, Central Eastern, and Southern
P. syriaca Boiss.	Caucasus and Middle East Region
P. taiwanensis Iketani and H. Ohashi	Taiwan
P. torminalis (L.) Ehrh.	North Africa, Middle East, South Caucasus, whole Europe
P. trilobata (Poir.) DC.	Israel, Lebanon, Turkey, Bulgaria, Greece
P. trilobata (Poir.) DC.	Turkey, Bulgaria, Greece, Israel, Lebanon
P. tschonoskii Maxim.	Japan
P. turkestanica Franch.	Kyrgyzstan, Tajikistan, Turkmenistan, Afghanistan
P. ussuriensis Maxim.	Russia, China, Japan, Korea, Brazil
P. vestita Wall. ex G. Don	China, Bhutan, India, Nepal, Myanmar
P. vilmorinii (C. K. Schneid.) Asch. and Graebn.	China
P. xerophila T. T. Yu	China
P. yunnanensis Franch.	China, Myanmar
P. zahlbruckneri (C. K. Schneid.) Cardot	China
P. × *bretschneideri* Rehder	China
P. × *complexa* Rubtzov	Former Soviet Union
P. × *hopeiensis* T. T. Yu	China
P. × *phaeocarpa* Rehder	China
P. × *serrulata* Rehder	China
P. × *sinkiangensis* T. T. Yu	China
P. × *uyematsuana* Makino	Japan, Korea

have supported that *Pyrus* is a monophyletic group containing two major clades that diverged far prior to any possible human intervention (Kim et al. 2015; Zheng et al. 2014; Korotkova et al. 2018; Wu et al. 2018). The first is an eastern Asian clade with a crown group age of 15.7 Mya, and the second is a western Eurasian clade that comprises species from Europe, Southwest Asia, and the Caucasus region, displaying a crown group of 12.38 Mya (Korotkova et al. 2018). The separation of these two clades may be related to the recession of the Turgai Strait, a Mesozoic epicontinental seaway that has separated Europe from Asia until the late Oligocene (Korotkova et al. 2018). However, Wu et al. (2018) have estimated that both clades diverged between 6.6 and 3.3 Mya. Their hypothetical common ancestor seems to have originated in China before dissemination through central Asia and then eventually on to western Asia and Europe (Wu et al. 2018). Within the western Eurasian clade, a major period of diversification has likely occurred in the Middle to Late Miocene when Caucasian and Southwest Asian lineages have diversified (Korotkova et al. 2018). Most of the extant diversity of *Pyrus* in western Eurasia appears to have originated in the Pliocene and the Pleistocene (Korotkova et al. 2018). *Pyrus* species diversity is concentrated in western Eurasia to eastern Asia, and particularly in China (Silva et al. 2014). Speciation in *Pyrus* is complex, and several currently accepted *Pyrus* species have not been recovered as monophyletic, thus indicating that current species limits require re-evaluation (Zheng et al. 2014; Korotkova et al. 2018).

Within the *Pyrus* genus, there are only a few species that have been domesticated for commercial production (Bao et al. 2007; Wu et al. 2013). Most cultivated *Pyrus* species include *P. communis* (European pear), and the Asian pear species of *P. ussuriensis* Maxim., *P. pyrifolia*, *P.* × *bretschneideri* Rehd., and *P. sinkiangensis* Yü (Wu et al. 2013; Ferradini et al. 2017). These have been domesticated from the following wild species, *P. communis* is derived from the wild European species *P. pyraster*, while the cultivated *P. ussuriensis* is derived from the wild *P. ussuriensis*, whereas *P. pyrifolia* and *P.* × *bretschneideri* are derived from the wild *P. pyrifolia* and finally *P. sinkiangensis* is derived from hybridization between the cultivated *P. communis* and either the cultivated *P. pyrifolia* or *P.* × *bretschneideri* (Wu et al. 2018). Although the majority of cultivated pears are diploid ($2n = 2x = 34$), a few cultivars of *P. communis* and *P.* × *bretschneideri* are known to be polyploids (Ferradini et al. 2017).

Currently, there are several studies aiming to estimate genetic distances among different pear cultivars/genotypes present in gene banks and in various breeding programs (Bao et al. 2007; Bassil and Postman 2010; Silva et al. 2014; Chang et al. 2017; Ferradini et al. 2017; Wu et al. 2018). Pear cultivars can be subdivided into two major groups, the occidental (European) and the oriental (Asian) pears, as confirmed by molecular data (Bao et al. 2007; Bassil and Postman 2010; Yue et al. 2014; Ferradini et al. 2017). European cultivars belong to *P. communis* and are most likely derived from one or two wild species, *P. pyraster* (L.) Burgsd. and/or *P. caucasica* Fed. (Ferradini et al. 2017). Therefore, European pear cultivars have a narrow genetic base (Miranda et al. 2010); whereas, cultivated pears native to East Asia belong to the following five groups, including the Ussurian pear (*P. ussuriensis*), Chinese white pear (*P.* × *bretschneideri*), Chinese sand pear (*P. pyrifolia*), Xinjiang pear (*P. sinkiangensis*), and the Japanese pear (*P. pyrifolia*) (Bao et al. 2007; Katayama et al. 2016). Phylogenetic studies of *Pyrus* cultivars native to East Asia have revealed contradictory results; thus, additional studies are required to resolve issues of origin and evolution of Asian pear cultivars (Bao et al. 2007; Bassil and Postman 2010; Iketani et al. 2012; Chang et al. 2017; Wu et al. 2018). However, Chang et al. (2017) have explored the evolution routes of *Pyrus* in China and highlighted the spread of pears from the Shanxi province to other regions of northern China. From China, pears were then disseminated throughout central Asia before they were spread over to western Asia and then on to Europe (Wu et al. 2018).

1.3.2.1 *Pyrus* Species in Western Eurasia

In general, occidental pears are distributed in Europe, northern Africa, Asia Minor, Iran, Central Asia, and Afghanistan (Zheng et al. 2014). They have been geographically divided into the following three subgroups: West Asian species, European species, and North African species

(Zheng et al. 2014; Zamani et al. 2017). It is reported that there are 12 primary species present in western Eurasia, including five European species (*P. communis*, *P. caucasica*, *P. pyraster*, *P. nivalis* Jacq., and *P. cordata* Desv.), five West Asian species (*P. elaeagrifolia* Pall, *P. spinosa* Forssk syn. *P. amygdaliformis* Vill., *P. regelii* Rehd., *P. salicifolia* Pall., and *P. syriaca* Boiss.), and three North African species (*P. cossonii* Rehd. syn. *P. longipes* Balansa ex Coss. & Durieu, *P. gharbiana* Trab., and *P. mamorensis* Trab.), while the remaining species are putative interspecific hybrids (Zheng et al. 2014). Further phylogeny studies have been conducted to characterize relationships among occidental primary species (Zheng et al. 2014). It is revealed that European species may be the latest derived occidental species and displaying lower levels of genetic diversity compared to West Asian species (Zheng et al. 2014). Moreover, European pears are most likely independently derived from West Asian species and North African species, as *P. nivalis* and *P. cordata* are more related to West Asian species, primarily to *P. spinosa;* whereas, *P. caucasica*, *P. pyraster,* and *P. communis* are more closely related to the North African species (Zheng et al. 2014). Among West Asian species, *P. regelii* is an early diverging and isolated species (Zheng et al. 2014), while the three African species are well differentiated with *P. gharbiana* and *P. mamorensis* and are more related to European species (Zheng et al. 2014).

It has been reported that wild occidental pears primarily inhabit two types of habitats, mesophytic forests and xerophytic open woodlands (Zamani et al. 2017; Korotkova et al. 2018). Xerophytic woodlands constitute a vegetation-type characteristic for arid and semi-arid regions of Southwest Asia, including the Caucasus ecoregion (Korotkova et al. 2018). Xerophytic woodlands likely play an important role in the diversification of *Pyrus* as these habitats comprise a considerable number of *Pyrus* species. The Caucasus ecoregion contains approximately 25 endemic species (Korotkova et al. 2018). Moreover, the majority of Caucasian pears inhabit xerophytic open woodlands and display morphological adaptations such as narrow leaves (Korotkova et al. 2018). The other remaining species mainly inhabit mesophytic forests and display broad leaves (Korotkova et al. 2018). Thus, wild pear species have diverged into numerous local ecogeographical races and species that are interfertile with the cultivated pear (Asanidze et al. 2011). It is important to point out that the country of Iran is also rich in *Pyrus* species, with about 23 taxa, and also has both xerophytic and mesophytic species (Zamani et al. 2017). These species occur throughout the north-east region through northern hyrcanian forests to the north-west (Azerbaijan province) and all the way to the southwest region in the Fars Province (Zamani et al. 2017).

The cross-compatibility among various *Pyrus* species raises questions on the taxonomy of *Pyrus* species (Zamani et al. 2017). For example, *P. caucasica*, an endemic species of the Caucasus, has been classified initially as a European pear, *P. communis*, but has been subsequently deemed as a separate species based on morphological differences of leaf margins (Asanidze et al. 2011). Although earlier studies have deemed *P. caucasica* as a completely independent species because of its morphological differences and its separate geographical distribution, it is now considered as a wild subspecies of *P. communis* (Asanidze et al. 2011). Furthermore, another wild ancestor of the cultivated European pear, *P. pyraster*, native to Eastern and Central European countries, including the Balkan Peninsula and Turkey, has also been considered either as a species or a subspecies of *P. communis* by different reports (Asanidze et al. 2011; Korotkova et al. 2018). Similar conflicting findings have been reported for other species, such as *P. balansae* Decne., *P. boissieriana* Buhse, *P. salicifolia*, *P. syriaca*, *P. georgica* Kuth., *P. demetrii* Kuth., *P. ketzkhovelii* S. Kuthath, and *P. sachokiana* Kuth. (Asanidze et al. 2011). Recently, Aydin and Dönmez (2015) have revised species taxonomy, present in Turkey, and have proposed species modifications. They have proposed that *P. pseudosyriaca* should be treated as a new botanical variety of *P. syriaca*, while *P. serikensis* and

P. boissieriana are reduced to synonyms of *P. cordata*, and *P. elaeagrifolia* Pall., respectively. In addition, subsp. *kotschyana* (Boiss.) Browicz is reassessed as *P. kotschyana* Boiss. ex Decne (Aydin and Dönmez 2015), while Zamani et al. (2017) have assessed the usefulness of biological markers to evaluate the taxonomic significance of Iranian pear taxa.

Pear improvement efforts undertaken in Europe have depended on *P. communis* and *P. nivalis*. Although *P. communis* is widely cultivated worldwide, its origin is not well understood. It is likely that *P. communis* may have other species in its genetic background, including *P. pyraster*, *P. caucasica*, *P. eleagrifolia*, *P. spinosa*, *P. nivalis*, and *P. syriaca* (Silva et al. 2014; Korotkova et al. 2018). On the other hand, *P. nivalis* is used in wine making and has been of great importance in both Britain and France for over 400 years (Silva et al. 2014).

1.3.2.2 *Pyrus* Species in East Asia

Oriental pears are distributed from the Tian Shan region and the Hindu Kush Mountains in Central Asia eastward to Japan (Zheng et al. 2014). There are nine proposed primary *Pyrus* species in East Asia, five have originated from China (*P. pyrifolia*, *P. ussuriensis*, *P. pashia* D. Don, *P. calleryana* Dcne, and *P. betulifolia* Bge), two from Japan (*P. dimorphophylla* Makino and *P. hondoensis* Yu), one from the Korean Peninsula (*P. fauriei* Schneid.), and one from Taiwan Island (*P. koehnei* Schneid.) (Zheng et al. 2014). The remaining species are most likely interspecific hybrids although their parentages remain uncertain (Zheng et al. 2014). In China, pear trees have originated in the mountainous regions of Southwestern China, and have spread both westward and eastward (Chang et al. 2017). A total of 69 *Pyrus* species are found in China. Of these, 13 have originated in China, including species with commercial cultivars, such as the Chinese white pear (*P.* × *bretschneideri*), Chinese sand pear and Japanese pear (*P. pyrifolia*), Sinkiang pear (*P. sinkiangensis*), and the Ussurian pear (*P. ussuriensis*) (Kell et al. 2015; Chang et al. 2017).

The Ussurian pear is mainly cultivated in North China, especially in Northeast China (Teng et al. 2015). The Chinese white pear is cultivated in North China and occupies the most important position in commercial pear production (Teng et al. 2015). The Chinese sand pear is naturally distributed in south China and owns plentiful cultivar resources (Teng et al. 2015). The Japanese pear refers to pears located in Japan, and has fruit traits similar to those of the Chinese sand pear (Teng et al. 2015). Wild *P. ussuriensis* is widely distributed in north-eastern China, eastern Russia, the Korean Peninsula, and central and northern Honshū in Japan (Iketani 2016). In Japan, two botanical varieties of *P. ussuriensis*, var. *aromatica* and var. *hondoensis,* are native to the northern area and the central area of the main island, respectively (Iketani 2016; Katayama et al. 2016). At least two native Japanese and one native Chinese *Pyrus* species, namely *P. ussuriensis, P. calleryana*, and *P. pseudopashia* T.T. Yu, are included in the National Red List (Kell et al. 2015; Iketani 2016). Early on, the Japanese pear is suspected to have originated from native plants in Japan; however, it is subsequently reported that *P. pyrifolia* is most likely introduced to Japan during prehistoric times (Iketani 2016).

Phylogeny studies have revealed incidence of close relationships among Asian *Pyrus* species. For example, Yue et al. (2014) have reported that the oriental pear cluster can be divided into two subgroups. One subgroup consists of three *P. betulifolia* accessions, while the other subgroup consists of all other cultivars and species, namely *P. pyrifolia*, *P. ussuriensis*, *P. pashia*, *P. dimorphophylla*, *P. fauriei*, *P. serrulata*, *P. hopeiensis*, *P. phaeocarpa*, *P. xerophila*, and *P. hondoensis*. Likewise, Zheng et al. (2014) have supported the existence of subclades for *P. ussuriensis* and *P. pashia,* but they have not resolve relationships among the remaining haplotypes. According to Wu et al. (2018), Asian pear accessions are clustered into the following four groups: a first large group that includes accessions of both *P.* × *bretchneideri* and *P. pyrifolia*; a second group that includes wild accessions of China, Japan, and Korea; a third group that clusters wild and cultivated accessions of *P. ussuriensis*; and a fourth group that includes all cultivated accessions of *P. sinkiangensis*.

Although genetic differentiation between groups of native populations and those of cultivars was usually high, cultivars were not well differentiated from each other (Iketani et al. 2012). The classification of cultivated pears could indeed be problematic due to cross-compatibility and introgression between species (Iketani 2016; Katayama et al. 2016). As for cultivated Asian pears, Bao et al. (2007) demonstrated that Chinese sand pears and Chinese white pears were clustered together, and that Japanese cultivars had sandy pears as parents, while Ussurian pears clustered separately (Bao et al. 2007). However, Bassil and Postman (2010) grouped Ussurian pear and Chinese white pear cultivars in the same clusters. According to Yao et al. (2010), some cultivars of Ussurian pear clustered with some Chinese white pears, while other Chinese white pears generally clustered with Chinese sand pear and Japanese pears. More recently, Chang et al. (2017) showed that Japanese sand pear and Chinese sand pear cultivars shared similar genetic backgrounds and exhibited a high degree of kinship. Earlier, Iketani et al. (2012) reported that Japanese pear cultivars had a simple genetic structure, while Chinese and Korean pear cultivars were admixtures of Japanese pear and native *P. ussuriensis*. Subsequently, Teng et al. (2015) showed that there were no real genetic differences detected among Chinese sand pear, Chinese white pear, and Japanese pear.

Globally, Asian pear cultivars have been deemed to be genetically continuous, and have a very narrow genetic diversity compared with that of wild species (Iketani et al. 2012). In this context, Iketani et al. (2012) have proposed that Asian pear cultivars should be regarded as a single group, although this may not be accepted by horticulturists. An alternative strategy is to divide Asian pears into four cultivar groups instead of species, namely *Pyrus* Ussurian pear group, *Pyrus* Chinese white pear group, *Pyrus* Chinese sand pear group, and the *Pyrus* Japanese pear group (Iketani et al. 2012).

1.4 Botanical Description of Pear

All *Pyrus* species are tree-like woody plants (Hedrick et al. 1921). They are medium-sized trees often with a tall, narrow crown, but with only a few species that are shrubby. Leaves are alternately arranged, simple, 2–12 cm in length, glossy green in some species, or densely silvery hairy in some others (Hedrick et al. 1921). Most pears are deciduous, but one or two species in Southeast Asia are evergreen. Flowers are usually white, borne in corymbs on short spurs, or on lateral branchlets (Hedrick et al. 1921). Flowers are about 2–4 cm in diameter, and have five sepals, five petals, numerous stamens, and five-locular ovary with usually free styles. The fruit is a pome, measuring 1–4 cm in diameter in wild species, and up to 18 cm in length and 8 cm in width in some cultivated forms (Hedrick et al. 1921). The form of the fruit varies in most species from oblate, or globose, to pyriform (Hedrick et al. 1921). The fruit is a pseudo-fruit composed of the receptacle, or a calyx tube that is greatly dilated and enclosing the true fruit, which consists of five cartilaginous carpels, known as the core (Hedrick et al. 1921). The flesh usually bears grit cells (sclereids) when ripened on the tree (Hedrick et al. 1921). Leaf and fruit traits are commonly used to distinguish among *Pyrus* species (Asanidze et al. 2011; Zamani et al. 2017). European pears are elongated and have full-bodied textures, while Asian pears are round in shape and have sandy textures (Silva et al. 2014).

Pear trees are self-incompatible, exhibiting typical gametophytic self-incompatibility, as with other Rosaceous species (Sassa et al. 2009; Franceschi et al. 2012). Gametophytic self-incompatibility is controlled by a single multi-allelic locus, the so-called *S*-locus. In Pyrinae, the *S*-locus contains the single pistil-side *S* determinant, the S-RNase, which is expressed