Compendium of Plant Genomes
*Series Editor:* Chittaranjan Kole

Timo Hytönen · Julie Graham · Richard Harrison
*Editors*

# The Genomes of Rosaceous Berries and Their Wild Relatives

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 70 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 Genomes of Rosaceous Berries and Their Wild Relatives

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ISSN 2199-4781 ISSN 2199-479X (electronic)
Compendium of Plant Genomes
ISBN 978-3-319-76019-3 ISBN 978-3-319-76020-9 (eBook)
https://doi.org/10.1007/978-3-319-76020-9

Library of Congress Control Number: 2018933473



Printed on acid-free paper

This Springer imprint is published by the registered company Springer International Publishing AG part of Springer Nature
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

*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 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 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, 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 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, evolution of the concepts, strategies, and tools of sequencing and bioinformatics reinforced the subject of genomics—structural and functional. Today, genome sequencing has traveled 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. 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, 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, eight crop and model plants, eight model plants, 15 crop progenitors and relatives, and three 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 is 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 both to 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, 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 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 long time 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 besides 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

Raspberries and strawberries are two of the major rosaceous soft fruit crops grown today with a global value in excess of $2bn worldwide. In recent years, these crops have lagged behind major agricultural staples in the genomic tools and resources available to them and comparatively little is known about the genomic architecture of berry crops and their wild relatives. This book, over 14 chapters, attempts to synthesize current research efforts into both wild relatives and rosaceous berry crops and highlight some of the most exciting developments in soft fruit breeding and genomics.

Chapter 1 gives an overview of the current economic importance of strawberry, the largest and most important rosaceous soft fruit crop, and charts production growth globally. It highlights the need for breeding solutions to the current high labour costs for harvesting, which is likely to play an increasing role globally in affordable horticultural produce. Chapter 2 places berry crops into their broader phylogenetic context and highlights the diversity in both *Fragaria* and *Rubus* families that remains largely unexplored in modern breeding.

Chapter 3 details the genomic resources available for the perennial model *Fragaria vesca*, detailing some of the genomic tools that have now arisen for crop species as a result of this more fundamental research. In the same vein, Chap. 4 focusses on the perennial cycle which has been elucidated to a fine level of detail in *Fragaria vesca* and is now being used to understand control of flowering in the octoploid strawberry. Similarly, studies of fruit quality using both near isogenic lines and other multiparental or association populations provide a promising mechanism to understand components of secondary metabolism which can then be used in crop species to improve quality. Disease resistance, again a key component of crop breeding programmes, often relies on families of genes involved in the perception of non-self or modified self. In Chap. 6, knowledge of the complement of some of the more common families of resistance genes is charted for *Fragaria* and *Rubus* genomes.

Moving into the crop systems, the remaining chapters all focus upon one or more aspects of rosaceous berry genomics. Carrying on the theme of disease resistance, Chap. 7 reviews the current state of research into diseases of the octoploid strawberry, describing the QTLs that are known for bacterial, fungal, and oomycete diseases. Chapter 8 does the same but for fruit ripening and fruit quality QTL. Chapters 9–12 all deal with cutting-edge approaches to breeding and genetics in the octoploid strawberry. Chapter 9 gives a comprehensive overview of the genotyping tools available for the octoploid strawberry and points to the use of new technologies for more cost-effective and rapid genotyping. Chapter 10 details progress on the octoploid sequence, utilizing some of the latest techniques such as 10X Chromium to untangle this complex crop genome. Chapter 11 provides both a historical perspective and future look towards the potential of genetic transformation in strawberry, highlighting the potential for genome editing as a tool for crop improvement. Finally, Chap. 12 details the use of genomic selection, a predictive breeding method in the octoploid. Taken together these techniques are set to revolutionize berry breeding in the coming decade.

Chapters 13 and 14 highlight the progress made in *Rubus* genomics and trait identification in recent years, with a report of the black raspberry genome in Chap. 13, and an overview of the biology of fruit development in red raspberry in Chap. 14.

It is hoped that this book gives an overview of the current status of berry genomes and highlights the enormous potential that this sector has to embrace modern technologies for crop improvement. We would like to thank each author for giving up their valuable time and for their efforts. We would also like to thank the series editor, Prof. Chittaranjan Kole, the editorial team at Springer for their assistance and also Angela Chapple for administrative assistance.

East Malling, UK — Richard Harrison
Helsinki, Finland — Timo Hytönen
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December 2017

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# 1 The Economic Importance of Strawberry Crops

David Simpson

**Abstract**

Strawberries are produced commercially in 76 countries. China is the largest producer and the top five producing nations also include USA, Mexico, Turkey and Spain. Production continues to increase, particularly in Asia, North and Central America, and North Africa with a matching increase in demand in many parts of the world. The development of the strawberry industry in California in the twentieth century was followed by rapid expansion of local industries in many other parts of the world including the Mediterranean region, Central and South America, Australia and China. In all of these regions, it was possible to identify the areas where a combination of short days with warm or mild temperatures made it possible to produce high yields over a long season. Plant breeding has had a very significant role in increasing the geographical adaptation of strawberries. The most notable achievement has been to transform the crop from a plant with a short season of production and a modest yield of small, soft berries to a highly productive plant capable of cropping over a long period with large, firm berries suitable for shipping over long distances.

Berries have been grown for food for over 2000 years and before that would have been an important part of the human diet when harvested from the wild. Commercial production of berries began to become important in the early part of the nineteenth century following the breeding of improved cultivars of the cultivated strawberry (*Fragaria* × *ananassa*), while raspberries followed several decades later in the century after the hybridisation of the European and North American sub-species of the red raspberry (*Rubus idaeus*). Both types of berry became important crops initially in western Europe and North America but were characterised by short seasons of only a few weeks. During the twentieth century, production gradually spread to many other parts of the world and berry crops steadily increased in their economic importance, particularly in the post-war period when improved cultivars and new agronomic practices resulted in an extension of the production season.

## 1.1 Strawberries

Worldwide production of strawberries exceeded 7.7 million tonnes in 2013, following an increase of 142% over the previous 20 years (FAOStat),

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T. Hytönen et al. (eds.), *The Genomes of Rosaceous Berries and Their Wild Relatives*, Compendium of Plant Genomes, https://doi.org/10.1007/978-3-319-76020-9_1

with commercial production in 76 countries covering all continents except Antarctica. China is the largest producer, with 3 million tonnes in 2013, and the top five producing nations also include USA, Mexico, Turkey and Spain. Strawberries are popular with consumers in nearly all parts of the world and the steady increase in global production had come about due to the adaptability of the species, which can be grown in anything from cool temperate to sub-tropical conditions, and the ingenuity of growers, scientists and agronomists in developing a variety of production systems to adapt to local conditions.

Breeding has been hugely significant in the success of strawberries. The first hybrids of *F.* × *ananassa* were produced in European gardens in the late eighteenth century, but breeding began in earnest in the ninetieth century and the cultivar 'Keens' Seedling', released in 1821, can be considered to be the first 'modern' strawberry. In nearly 200 years of subsequent breeding, the most notable achievement has been to transform the strawberry from a plant with a short season of production and a modest yield of small, soft berries to a highly productive plant capable of cropping over a long period with large firm berries suitable for shipping over long distances. A notable example of this has been the progress achieved in the last 70 years by the breeding programme at the University of California. Cultivars were developed that both extended the range of the production area within the state and greatly increased the length of the production season. A comparison of the cultivars released in 1945–1966 with those released 1993–2004 showed yield, fruit size and firmness increased by factors of 2.4, 1.7 and 1.9, respectively (Shaw and Larson 2008). These cultivars have helped California establish its dominant position in US production, where it currently supplies 88% of the market for fresh and frozen strawberries, and the value of the California strawberry crop was approximately $1.6 billion in 2015 (California Department of Food and Agriculture). Furthermore, the example from the development of the industry in California led to similar expansion of local industries in many other parts of the world including the Mediterranean region, Central and South America, Australia and China. In all of these regions, it was possible to identify areas where a combination of short days with warm or mild temperatures made it possible to grow the UC cultivars successfully, demonstrating the great adaptability of strawberry plants. Most countries also have local breeding programmes, developing cultivars that are specifically adapted for the climatic conditions and the market, but there are now also large international breeding companies such as Driscoll's who have breeding programmes covering many countries across six continents.

The fact that strawberries are produced in 76 countries is an indication of their popularity with consumers worldwide but also demonstrates their value to many different local economies. Despite great advances in extending shelf life and cool chain marketing, the fresh berries remain a perishable crop that needs to be produced close enough to the market to avoid excessive transport costs. This is in contrast to many tree fruit crops, which can be successfully stored for long periods and thus shipped worldwide, resulting in production being focussed in regions that are geographically suited to produce high yields at a relatively low cost per unit. The situation is different with perishable berry crops because there is often a good economic rationale for production even in marginal areas. Harvesting of dessert strawberries is currently all done by hand, and this makes the crop labour intensive, particularly during the harvest season. In turn, this provides employment and benefits the local economies in the production regions. In some countries local labour is readily available for harvesting, but in others, such as North America and Western Europe, there is a heavy reliance on migrant labour with the workers often staying on the fruit farms in temporary accommodation for the duration of the season.

### 1.1.1 Global Production

Between 2004 and 2013, the world production of strawberries increased by 41% (Table 1.1),

**Table 1.1** Strawberry production in the main growing regions (tonnes)

| Country or region | 2013 | 10-year trend (%) |
|---|---|---|
| World | 7,739,622 | +41 |
| China | 3,005,304 | +61 |
| USA | 1,360,869 | +36 |
| European Union | 1,125,552 | +2 |
| Mexico | 379,464 | +114 |
| Turkey | 372,498 | +140 |
| Egypt | 254,921 | +143 |
| South Korea | 216,803 | +7 |
| Russia | 188,000 | −9 |
| Japan | 160,237 | −19 |
| Morocco | 145,233 | +37 |

*Source* FAOStat

indicating both the growing economic importance of the crop and the growing demand from consumers. Mexico, Turkey and Egypt are the three countries to have shown the greatest increase over this period, and this demonstrates a trend for production to shift to countries that have climates offering long growing seasons combined with readily available labour at relatively low cost and proximity to large domestic or export markets.

#### 1.1.1.1 North and Central America

For many decades, the USA was the world's largest producer of strawberries before being overtaken by China in 1994. Production is focussed in two states that have an ideal climate and soils for strawberries with California producing 88% of the total crop and Florida 9%. Jointly, these two states are able to supply the US market year-round. The domestic market is very strong with per capita consumption almost doubling over the last two decades due to consumers having increased awareness of the health aspects of eating berries coupled with an improved year-round availability. Annual consumption was 4.5 kg per person in 2014 (USDA-NASS) of which 3.6 kg was fresh fruit and 1.4 kg frozen. From 1995 to 2014 the US population increased by 20% to 319 million (US Census Bureau), which combined with the increased consumption resulted in the market increasing by 132%. Over the same period production increased by 107%, with most of the balance provided by imports from Mexico who supply over 99% of the imported fresh fruit and 82% of frozen strawberries. The USA is a net importer of strawberries but still exports 11% of its production, with Canada being the main market for fresh and frozen berries and Japan also receiving significant volumes of frozen.

California and Florida both have breeding programmes in the public and private sectors. These programmes have been very successful in developing cultivars that have been successful not only in these two states but in many other regions throughout the world, thus providing an important income stream from plant or fruit royalties returned to the breeders. In particular, cultivars released from the programmes at the Universities of California and Florida are grown throughout the world and have often been used to start large-scale strawberry production in regions that have not previously grown strawberries on a significant scale. These cultivars then often form the base germplasm for new breeding programmes designed to develop cultivars with improved local adaptation.

Strawberry growing in Mexico has increased greatly in the twenty first century, and it is now the world's third biggest producer. The main strawberry growing regions are Michoacan and Guanajuato in central Mexico and Baja

California in the northwest (Wu et al. 2012). Mexico typically exports 30–45% of its crop, making it the world's third largest exporter of fresh strawberries, and most of it is shipped to the USA. The season in Mexico commences earlier than California, thus providing a good export opportunity, but the seasons overlap considerably, and the rapid recent increase in Mexican imports has led to an oversupply of strawberries on the US market in some years. Most of the cultivars grown in Mexico originate from California and are a mixture of proprietary cultivars and those developed by the University of California.

#### 1.1.1.2 European Union

Strawberries are produced in 26 countries within the European Union (EU) but Spain, Poland and Germany account for 58% of the production (FAOStat), while the leading nine countries produce 90% of the total (Fig. 1.1). Average per capita consumption is 5 kg (Binard 2016), slightly higher than the USA (4.5 kg), but this has remained fairly constant, and consequently the production has only increased by 2% over the 10 years to 2013 (Table 1.1). There is a high level of trade between countries within the EU, amounting to 37% of total production, and the two largest producers export high volumes. Spain has 28% of EU production at 312,500 tonnes but 83% of this is exported, mainly as fresh berries during the period February to May when the main market is in northern Europe, particularly Germany, France and the UK. Poland has 17% of EU production and is also a large exporter, but their 80% of the production is for the processing sector, with exports mainly as frozen berries which are used as the raw material for jams, dairy products and other processed foods.

Germany, France and the UK are the main importers within the EU market, and each of these also has a significant volume of home production. These countries represent strong

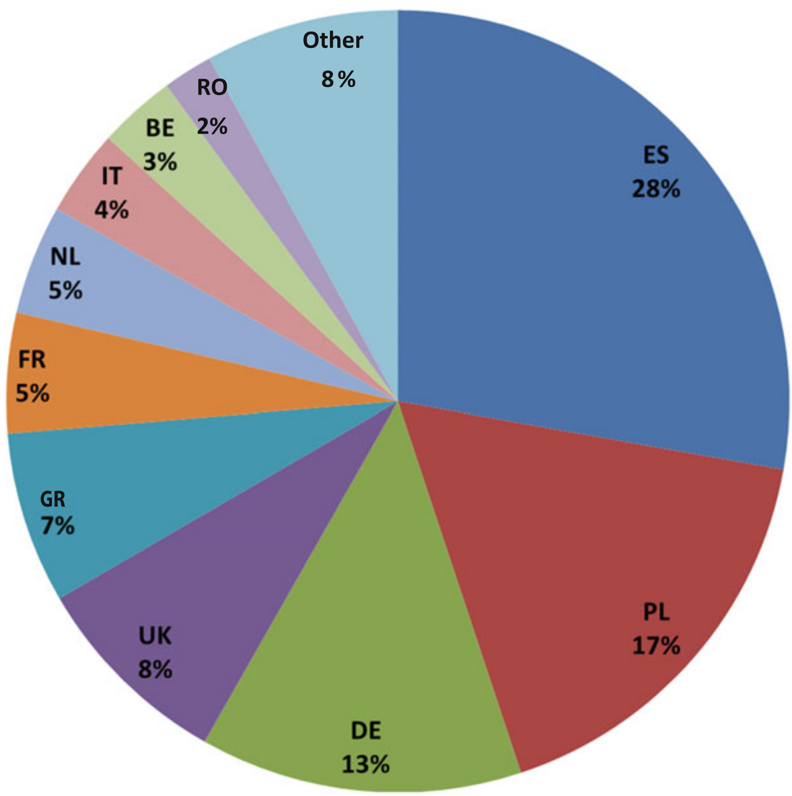


**Fig. 1.1** Strawberry production in the European Union. The contribution of each country to the total production volume (tonnes) is shown (FAOStat 2013)

markets, which have been growing, but the per capita consumption is still below average for France and the UK at 3.8 and 3.5 kg per annum, respectively. Imports to and exports from the EU are relatively small compared to the internal trade. In 2013, imports of c. 29,000 tonnes were equivalent to less than 3% of the EU production with most fruit coming from Morocco and Egypt who can supply the market during the winter, before the Spanish season commences. Exports outside the EU account for 6% of total production, with the main markets being other European countries that are not members of the EU (Binard 2016).

There are many strawberry breeding programmes in the EU, in both the public and private sectors. All of the main producing countries have at least one significant programme and in many countries there are several. In the Mediterranean countries, production is based on low chill cultivars that will crop over a long period in late winter and early spring. Cultivars developed by the local programmes compete with those bred in California or Florida, and there is strong competition between the many programmes, resulting in a high turnover of cultivars. The cultivars grown in southern Europe are not adapted in the north, where the colder winters favour cultivars with a higher chilling requirement. Large, successful breeding programmes in France, Holland and the UK have produced most of the cultivars grown in northern Europe, but some cultivars from North America have also been successful, notably day-neutral types.

#### 1.1.1.3 Asia

China is by far the world's largest producer of strawberries, but South Korea and Japan are also big producers in East Asia. Chinese production increased by 61% in the 10 years to 2013 and is now more than the combined output from North America and Europe. China is such a large country that it encompasses a wide range of different climates, but most strawberry production is concentrated in winter and spring, using low-chill short-day cultivars. However, demand outside this period has recently led to an increase in summer and autumn production using day-neutral cultivars. The main production regions are in the Liaoning, Sichuan, Shandong, Anhui and Hebei provinces (Zhang pers. comm.), which covers a geographical range from 30°N to 42°N, thus providing for a long season of production. Most of the crop is grown under protection from polytunnels or traditional Chinese greenhouses. These growing regions provide good proximity to the large cities and centres of population in central, eastern and north China, and 95% of the production is for the fresh market. Chinese consumers prefer strawberries with a high sugar content combined with low background acidity, and consequently the cultivars bred in Japan are preferred to those originating from the USA or Europe, where a different sugar:acid balance is preferred. Cultivars developed abroad currently dominate in China but in recent years there has been a significant increase in breeding activity, in both the public and private sectors, and successful Chinese-bred cultivars are increasing their market share.

Japan has a long history of strawberry growing, dating back to the 1880s, and it became a major producer from the 1950s. FAO statistics began in 1961, and from then until 2000 Japan was consistently in the top three strawberry producing countries worldwide. However, in the twenty-first century Japanese production has declined and it currently ranks ninth in the world, having been overtaken by some of the countries that have rapidly increased their production such as China, Mexico, Turkey and Egypt. The decline in production is attributed to demographic changes, such as ageing farmers and lack of successors, combined with lower per capita consumption (USDA GAIN report 2015), which reduced by 30% from 2000 to 2013. Nevertheless, strawberries remain a very popular fruit in Japan and, with negligible exports, virtually all the production is of fresh berries that are consumed within the country. In the 1960s, Japan developed a forcing technique for strawberries that was particularly well adapted for their climate (Yoshida 2013), and currently the growers are almost exclusively using Japanese-bred short-day cultivars that were developed for this system. The main season is from December to

May with virtually all production in glass or plastic greenhouses. This winter production is concentrated on the islands of Honshu and Kyushu, and in addition, there is a small amount of summer production on Hokkaido using ever-bearing and day-neutral cultivars. Imports of fresh strawberries to Japan are on a small scale, but in 2014 over 3000 tonnes were imported from the USA from July to November and mainly used in the confectionery trade. Imports of frozen berries are much larger, at over 30,000 tonnes, with China being the main source.

Strawberry growing in South Korea shows similarities with Japan as it has a large production of fresh berries of which 98% is consumed domestically. However, unlike Japan, the production in South Korea is increasing, with a growth of 7% in the 10 years to 2013. Around 97% of strawberries are grown in greenhouses with the peak production period being from January to March. Most of the production is in the central and southern regions of the country with Gyeongsangnam-do and Chungcheongnam-do provinces producing 66% while Jeollanam-do and Jeollabuk-do provinces produce around 20%. Until 2005, Japanese-bred cultivars were dominant, but in the last 10 years this situation has changed dramatically with now over 80% of production using cultivars bred in South Korea. The cultivars show similarities to those from Japan, being low-chill short-day types that are adapted to forcing and have a high sugar content combined with low acidity.

In west Asia, Turkey is the main strawberry producer. Strawberries have been grown in Turkey since the nineteenth century, but modern strawberry production is considered to have started in the 1980s when high-yielding cultivars were imported from California. There has been approximately a tenfold growth in production since that time, with an increase of 140% and in the 10 years to 2013 (Table 1.1). The main growing areas are the Mediterranean, Aegean and Marmara regions with the season covering winter and early spring (Kafkas 2017). Around 80% of production is under protection from low or high tunnels with the focus on high-quality fresh berries, but towards the end of the season the fruit is harvested for freezing and other industry uses. Approximately 90% of the fruit is consumed domestically with the remainder exported, mainly as fresh berries with the main markets being eastern Europe and Ukraine. Some Turkish-bred cultivars are grown, but this is on a fairly small scale, and most of the production is using cultivars from Florida, California and Australia.

### 1.1.2 Future Prospects

Strawberry production and consumption have increased dramatically in the twenty-first century, and this trend looks set to continue. China, for example, has experienced a huge increase in consumption of fresh strawberries running in parallel with strong economic growth, and it is likely that this trend will be repeated in other countries with rapidly developing economies, such as Brazil and India. Developments achieved through breeding and innovative agronomic systems have made fresh strawberries available throughout the year, so they are no longer considered a seasonal crop by consumers. Their popularity continues to increase in most countries because they are considered to be a healthy food that is affordable, pleasant to eat and requiring minimal preparation. The challenge facing producers will be to meet the increasing demand in a sustainable and cost-effective way. The largest cost in production is harvesting, which for all dessert berries is done by hand and this presents a challenge in countries where agricultural wages are high. Many countries rely on migrant labour for harvesting, but this can bring problems with availability of staff, provision of accommodation and political issues. Unsurprisingly, there has been a trend for production to move to countries where labour costs are lower, although these are typically further away from the main markets and long-distance shipping of perishable berries can be problematic and expensive. A possible solution to this problem could be provided by robotic harvesting, particularly for strawberries grown in glasshouses