Compendium of Plant Genomes
*Series Editor:* Chittaranjan Kole

Ryutaro Tao
Zhengrong Luo *Editors*

# The Persimmon Genome

Springer

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**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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*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 F2 were utilized and a number of computer programs were developed for map construction, mapping of genes, and 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 by 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, 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 the 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 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. The development of software for 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, 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 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, a 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 of 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 lifetime experience and expertise in 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, particularly Dr. Christina Eckey and Dr. Jutta Lindenborn for the earlier set of volumes and presently Ing. Zuzana Bernhart for all their timely help and support.

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 to this compendium to them will suffice to do justice to their sacrifices for the interest of science and the science community.

New Delhi, India Chittaranjan Kole

# Preface

The genus *Diospyros* includes about 500 species, which accounts for the largest genus of the family Ebenaceae. Most of the *Diospyros* species are distributed in the tropical and subtropical regions of the world. Some of the tropical *Diospyros* species are used as ebony wood. The temperate species, such as *D. kaki*, *D. oleifera*, *D. lotus*, *D. rhombifolia*, and *D. virginiana*, have horticultural and economic importance. *D. lotus* is generally cultivated as rootstock, while *D. oleifera* is mainly used to obtain persimmon oil (kaki tannins) in China. *D. rhombifolia* is an ornamental shrub in East Asia. *D. virginiana* is native to the Eastern USA and eaten as fresh or used as rootstock. *D. kaki*, often referred to as simply kaki, or Japanese or oriental persimmon, is a major commercial species for fruit production. *D. kaki* originated in China and has been cultivated for a long time in the East Asian countries. Recently, this fruit species has been cultivated as a new and exotic fruit in Italy, Spain, Brazil, Israel, Azerbaijan, and Uzbekistan. The total amount of persimmon production has been increasing constantly every year these days. More than 2000 accessions of persimmon are preserved in China, Japan, Korea, Italy, Spain, and some other countries.

The species with precise chromosome numbers account for approximately 10% of the total *Diospyros* species. Most of the diploid species were found in the tropical or subtropical zone of the globe, while polyploid species, including *D. kaki*, are distributed in temperate regions. High ploidy (2n = 6X or 9X = 90 or 135) level of *D. kaki* is often an obstacle to efficient genetic studies for a long time. However, the recent advancement in molecular biology and DNA sequencing technologies opens the door for the utilization of genomic and genetic approaches to study and improve this species.

We here have compiled the book *The Persimmon Genome* with contributions from eminent persimmon researchers from Italy, Spain, Japan, and China to summarize the latest information on persimmon studies with a special reference to the recent status of persimmon genome studies. Each chapter of this book well describes respective aspects of conventional, molecular, and genomic studies in *Diospyros*. Although persimmons had been long regarded as an East Asian exotic fruit tree, it is now becoming a worldwide fruit tree. As the editors of this book, we hope that this book will make more scholars become interested in persimmon research, and expand the scope of persimmon production and research.

Kyoto, Japan — Ryutaro Tao
Wuhan, China — Zhengrong Luo

# Contents

# Abbreviations

| | |
|---|---|
| ADH | Alcohol Dehydrogenase |
| AIC | Akaike Information Criterion |
| ALDH | Aldehyde Dehydrogenase |
| ANR | Anthocyanidin Reductase |
| ANS | Anthocyanidin Synthase |
| AST | Astringency |
| BA | Benzyl Adenine |
| BAC | Bacterial Artificial Chromosomes |
| C | Catechin |
| CDS | Coding Sequence |
| CEGMA | Core Eukaryotic Gene Mapping Approach |
| CG | C-3-O-gallate |
| CHI | Chalcone Isomerase |
| CHS | Chalcone Synthase |
| CNR | Cell Number Regulator |
| C-PCNA | Chinese PCNA |
| cpDNA | Chloroplast DNA |
| CPPU, KT30 | N-(2-Chloro-4-pyridyl)-N′-phenylurea |
| CTs | Condensed Tannins |
| DEG | Differential Expressed Gene |
| DEMs | Differentially Expressed miRNA |
| DFR | Dihydroflavonol 4-reductase |
| EC | Epicatechin |
| ECG | EC-3-O-gallate |
| EGC | Epigallocatechin |
| EGCG | EGC-3-O-gallate |
| F | Inbreeding Coefficient |
| F3′5′H | Flavonoid 3′5′-hydroxylase |
| F3′H | Flavonoid 3′-hydroxylase |
| FAOSTAT | Statistics Division, Food and Agriculture Organization of the United Nations |
| FISH | Fluorescent in Situ Hybridization |
| FWs | Fruit Weights |
| GC | Gallocatechin |
| GCG | GC-3-O-gallate |

| | |
|---|---|
| GISH | Genomic in Situ Hybridization |
| GO | Gene Ontology |
| HKT | High-Affinity Potassium Transporter |
| HPLC–ESI–MS/MS | High-Performance Liquid Chromatography–Electrospray Ionization Tandem–Mass Spectrometry |
| HTN | Hiratanenashi |
| IR | Identical Inverted Repeat Regions |
| IRAP | Inter-Retrotransposon Amplified Polymorphism |
| ISSR | Inter-Simple Sequence Repeat |
| ISTR | Inverse Sequence-tagged Repeat |
| ITS | Internal Transcribed Spacer |
| IVIA | The Instituto Valenciano de Investigaciones Agrarias, Spain |
| J-PCNA | Japanese PCNA |
| KEGG | Kyoto Encyclopedia of Genes and Genomes |
| LAR | Leucoanthocyanidin Reductase |
| LSC | Large Single-Copy Region |
| LTR | Long Terminal Repeat |
| MAS | Marker Assisted Selection |
| MBW | MYB-bHLH-WD40 Complex |
| MDGR | Male Diospyros spp. Germplasm Resources |
| MeGI | Male Growth Inhibitor |
| ML | Maximum Likelihood |
| MP | Maximum Parsimony |
| MpV | Mid-parental Value |
| MSY | Male-Specific Region of the Y-chromosome |
| mtDNA | Mitochondrial DNA |
| NARO | The National Agriculture and Food Research Organization, Japan |
| NFGP | National Field Genebank for Persimmon |
| NGS | Next Generation Sequencing |
| NHX | $Na^+/H^+$ Exchanger Family |
| non-PCA | Non-PCA |
| non-PCNA | Non-PCNA |
| OGI | Oppressor of MeGI |
| PAL | Phenylalanine Ammonia-lyase |
| PAR | Pseudoautosomal Regions |
| PAs | Proanthocyanidins |
| PCA | Pollination Constant & Astringent |
| PCD | Programmed Cell Death |
| PCNA | Pollination Constant & Non-Astringent |
| PDC | Pyruvate Decarboxylase |
| PHYLIP | Phylogeny Inference Package |
| PK | Pyruvate Kinase |
| PVA | Pollination Variant & Astringent |
| PVNA | Pollination Variant & Non-Astringent |
| QTL | Quantitative Trait Locus |
| RAD seq | Restriction Site Associated DNA Sequencing |

| | |
|---|---|
| RAPD | Random Amplified Polymorphic DNA |
| REMAP | Retrotransposon-microsatellite Amplified Polymorphism |
| RFLP | Restriction Fragment Length Polymorphism |
| SCAR | Sequence Characterized Amplified Region |
| SCoT | Start Codon Targeted |
| SCTs | Soluble Condensed Tannins |
| SiMeGI | Sister of MeGI |
| SMRT | Single-Molecule Real-Time |
| SNP | Single Nucleotide Polymorphism |
| SOS | Salt Overly Sensitive |
| SRAP | Sequence-Related Amplified Polymorphism |
| SSAP | Sequence-Specific Amplified Polymorphism |
| SSC | Soluble Solids Concentration |
| SScR | Small Single-copy Region |
| SSR | Simple Sequence Repeat |
| TBR | Tree-Bisection-Reconnection |
| TDZ | Thidiazuron |
| TEs | Transposable Elements |
| TFs | Transcription Factors |
| TRAP | Targeted Region Amplified Polymorphism |
| TTN | Totsutanenashi |
| WAB | Weeks after Bloom |
| WGCNA | Weighted Gene Coexpression Network Analysis |
| WGD | Whole-Genome Duplication Events |
| WPGR | Wild Persimmon Germplasm Resources |
| WUE | Water Use Efficiency |

# History and Current Status of Worldwide Production

1

Edgardo Giordani

**Abstract**

Persimmon is cultivated in many regions of the globe. Worldwide yearly production is increasing in absolute values and in comparison with other fruit species since 1961. FAOSTAT Database reports for 2019, a production of 4,270,074 t, an area harvested of 992,425 ha, and an average yield of 4.3 t/ha. Asia is the continent showing the highest contribution to persimmon production (about 87%), followed by Europe (almost 10%), America (3.5%), and Oceania (less than 1%); no data are reported in the FAOSTAT Database for Africa. Americas and Europe show an increasing trend of yields since the year 2000 with the highest value in 2017 (22.1 t/ha), in Oceania, the values are lower (about 12 t/ha), while the lowest and constant yields (about 4 t/ha) were observed for Asia. The countries producing more than 10,000 t of persimmons per year from FAOSTAT Database in 2019 are China (3,092,000 t), Spain (404,131 t) Korea (298,382 t), Japan (224,900 t), Brazil (182,185 t), Azerbaijan (147,219 t), Uzbekistan (88,233 t), Italy (49,675 t), Israel (29,000 t), and Iran (24,257 t). In most of those countries, the trend of production is increasing, with the exception of Japan, Italy, and Mexico. The persimmon contribution to total fruit production at a global level is increasing (from 0.32% to 0.52% in years 1985 and 2015, respectively) and Azerbaijan, Korea, and Japan are the countries with the highest values (from 4% to almost 10%). Persimmon is placed 18th (after strawberries, dates, and avocado and before kiwifruits, apricots, and cherries, among others) in the list of 33 fruit crops itemized in the FAOSTAT Database for the year 2015.

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## 1.1 Introduction

Persimmon is the common word adopted to indicate in the English language, the botanical species *Diospyros kaki* Thunb. Nevertheless, the origin of this term seems to be ascribable to North American native Algonquin language to indicate *Diospyros virginiana* L., known as American persimmon. *Diospyros kaki* is also termed as Kaki and Oriental persimmon. In this chapter, both persimmon and kaki will be used in reference to *D. kaki* Thunb., that represents by far the most important crop for which official production data is available, while the amount of fruits of *D. virginiana*, *D. lotus,* and other *Diospyros* species with edible fruits are negligible when compared to the first one.


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This chapter illustrates persimmon production data gathered from the FAOSTAT Database (FAOSTAT, 2021), with some integration obtained from published documents and personal communications. Fruit production (in metric tons), harvested surface (in hectares), and yield (metric tons/ha) will be the items of discussion. The series of data available from FAOSTAT Database from 1961 to 2019 allows to have quite a clear picture of the evolution of the cultivation and production of persimmon in quantitative terms, nevertheless, limitations of the results due to the possible absence of data and/or of data estimations at country level, must be acknowledged.

## 1.2 Origin and Early Diffusion

China is recognized as the center of origin and first diffusion of persimmon, where it is widely distributed in most provinces, except the cold areas (Zhang et al. 2018). The retrieval of charred seeds in the Neolithic Tianluoshan site in the lower Yangtze River valley suggests very ancient use of persimmon fruits in that Chinese geographic area (Gupta et al. 2013). Ancient written and painted records of the use of persimmon show that this crop is present since many centuries in Japan and Korea (Yamada 2005; Yamada et al. 2012). *Diospyros kaki* seems to have diffused toward western areas of the Euro-Asiatic continent through caravans along the Silk Road, reaching Turkey, and probably the Mediterranean area in ancient times. Successively, Spanish and Portuguese colonial trades and migrations from oriental countries expanded the diffusion of persimmon to the Americas, Europe, and Oceania. In the last sixty years, globalization has augmented the transport of propagation material for the planting of many fruit crops, including persimmon (Hulme 2009), hence this species spread in many areas of the world with adequate climatic conditions.

## 1.3 Evolution of the Worldwide Production

Worldwide, the yearly production of persimmon fruits was about 1,000,000 tons in the decades 1960, 1970, and 1980, overcoming 4,270,000 t from 2012 up to 2019 (Fig. 1.1). Within this lapse of time, the yearly amounts of produced persimmons are highly correlated ($r = 0.97$) to those of the overall fruit production ("Fruit primary" aggregated group in the FAOSTAT Database); a similar correlation was also observed for the area harvested ($r = 0.93$). The production increase fourfolds the initial amounts of 50 years ago is confirmed by the raw data and the linear trend line (Fig. 1.1). Such relevant evolution in quantitative terms can be attributed to the actual increase of production and the inclusion of the statistics of persimmon production of new countries in the FAOSTAT

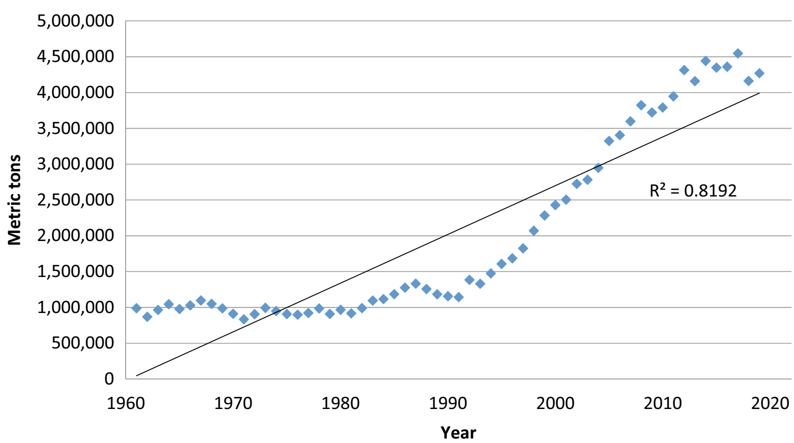


**Fig. 1.1** Trend of worldwide persimmon production in the last sixty years (FAOSTA, 2021)

Database. For instance, during the period 1960–1970, the number of countries contributing to persimmon production as from FAO statistics was 6 (China mainland, China-Taiwan, Brazil, Italy, Japan, and Republic of Korea), 9 in the successive decade, and 17 after the year 2017. Taking into account that in some cases yearly data can be referred to estimations, fluctuations of production between one year and the successive resulted close to zero in many cases, while reaching percentages of plus or less than 10–12% in other consequent years. The persimmon area harvested in the 1960 decade was about 160,000 ha; it overcome 500,000 ha in year 2000 and reached almost 1,000,000 ha in 2019. The correlation between persimmon production and area harvested is linear (r = 0.99), thus showing a steady trend in the last sixty years of persimmon yields (∼5 t/ha) as from FAO statistics. Indeed, this value does not represent the actual usually observed yields of persimmon orchards of most countries, which ranges from 15 up to 50 t/ha.

## 1.4 Evolution of the Production Among Continents

Persimmon is spread over the five continents, nevertheless, the amount of production widely varies among them taking into account FAOSTAT data. Figure 1.2 shows the contribution in percentage of each continent in year 2019. There is no FAOSTAT data for persimmon production in Africa, while Asia is by far the continent with the highest production all along the five decades of available data with about 1,000,000 t of yearly production in the decade 1960–1970 and over 4,000,000 t in the last few years. Europe is the second-largest producer continent, with over 300,000 t in the last five years and a very significant increase of yearly production since year 2000 substantially due to the Spanish production. The American continent is producing almost 170,000 t/year, with an increment of 0.18 t/year since the 1960 decade, reaching almost 200,000 t in 2015 but showing a minor reduction of production in the last few years. The first statistic data on persimmon production in Oceania is dated 1983 (less than 100 t), its yearly production reached the maximum amount in the years 2000 (almost 4000 t/year) while it was below 3000 t during the last three years.

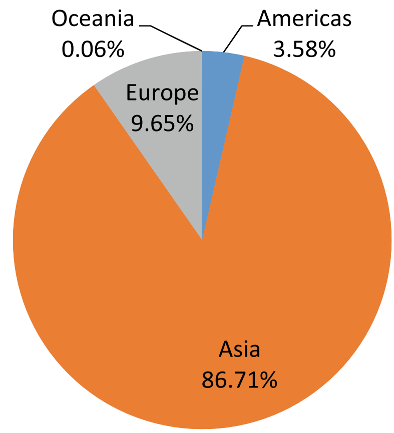


**Fig. 1.2** Contribution of continents in the persimmon production in year 2019 (FAOSTA, 2021)

Yields (Fig. 1.3) are different among continents; Americas and Europe show an increasing trend since year 2000 with the highest values in 2017 (21.6 and 22.1 t/ha, respectively), while in Oceania the values are lower (from 7 to 12 t/ha); the lowest and stable yields (about 4 t/ha) from FAOSTAT data were found for Asia.

The amount of countries contributing to the continental production is increasing with time; during the period 1990–2015, the new entries were Chile in Americas, Uzbekistan in Asia,

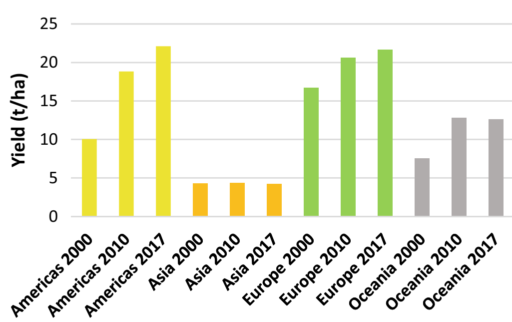


**Fig. 1.3** Trend of average yields of persimmon orchards in Americas, Asia, Europe, and Oceania (FAOSTAT, 2019)

Azerbaijan, Spain, and Slovenia in Europe (FAOSTAT, 2021).

## 1.5 Evolution by Country

The evolution of the persimmon production by country is often hindered by the lack of available data. Indeed, FAOSTAT includes official data transmitted by countries but, as an example, Spain was not included in the FAO statistics for many years, even when its persimmon production was relevant at the national level, but also in reference to the worldwide production. In this section, production by country takes into account official data from FAOSTAT Database.

### 1.5.1 Persimmon Production in Asian Countries

Among the countries where persimmon is traditionally cultivated and production statistics are present in FAOSTAT Database since 1961, China (Fig. 1.4) is showing the highest yearly production in the world (3,247,068 t on a harvested area of 992,425 ha in 2019, contributing to 76% to the worldwide production) with a yearly average increase of 55,000 t/year from 1961 to 2019 and 87,000 t/year in the period 1990–2019.

The persimmon production trend in Korea (Fig. 1.5), a country with a pluricentennial tradition of cultivation of this crop, shows an increase of about 2300 t/year between 1960 and 1980 followed by a more relevant growth rate (about 10,000 t/ha) between 1980 and 2000, year in which the production resulted close to 300,000 t. In the last 20 years, the Korean persimmon production oscillated widely among years, from about 249,000 in 2003 to 430,000 t in year 2008, being the latter the highest production amount ever registered for this country. In 2019, the production reached 316,042 t with a yield of 12 t/ha (FAOSTAT, 2019).

Persimmon cultivation in Japan started very old time, nevertheless, the evolution of persimmon production in Japan in the last sixty years is characterized by a negative trend (Fig. 1.6). The average Japanese persimmon production in the decade 1960 was about 414,000 t/year, while from 2010 to 2019, it is 225,000 t/year, with a maximum value of 504,400 t in 1967 and a minimum in the year 2010 (198,400 t). The average yield of the two periods taken into account resulted constant (about 11 t/ha as from FAOSTAT Database).

Uzbekistan's statistics on persimmon production in FAOSTAT (Fig. 1.7) start from year 2000 with 16,000 t while the 2019 harvest reached 94,065 t, with a positive trend of production increment, as well as of yield (from about 6 t/ha to about 20 t/ha, in 2000 and 2019, respectively).

The trend of persimmon production in Israel is positive since 1975 (Fig. 1.8), which is the first year of data reported in the FAO Database. Starting from about 8200 t/year during the first decade of available data (1975–1985), in the last decade (2010–2019) the average yearly

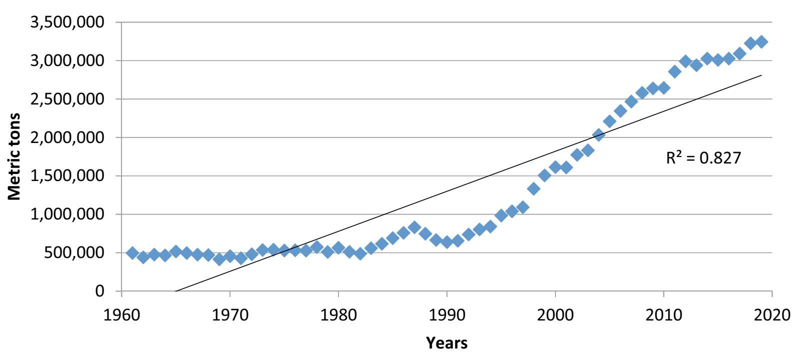


**Fig. 1.4** Persimmon production trend in China (FAOSTAT, 2021)