

Compendium of Plant Genomes
Series Editor: Chittaranjan Kole

Masayoshi Shigyo · Anil Khar
Mostafa Abdelrahman *Editors*

The Allium Genomes

Compendium of Plant Genomes

Series editor

Chittaranjan Kole, Raja Ramanna Fellow, Department of Atomic Energy,
Government of India, Kalyani, Nadia, West Bengal, India

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.

Interested in editing a volume on a crop or model plant? Please contact Dr. Kole, Series Editor, at ckole2012@gmail.com

More information about this series at <http://www.springer.com/series/11805>

Masayoshi Shigyo · Anil Khar
Mostafa Abdelrahman
Editors

The Allium Genomes

 Springer

Editors

Masayoshi Shigyo
College of Agriculture, Graduate School
of Sciences and Technology for
Innovation
Yamaguchi University
Yamaguchi, Japan

Mostafa Abdelrahman
Laboratory of Molecular Breeding
Arid Land Research Center
Tottori University
Tottori, Japan

Anil Khar
Division of Vegetable Science
ICAR-Indian Agricultural Research
Institute
New Delhi, India

ISSN 2199-4781 ISSN 2199-479X (electronic)
Compendium of Plant Genomes
ISBN 978-3-319-95824-8 ISBN 978-3-319-95825-5 (eBook)
<https://doi.org/10.1007/978-3-319-95825-5>

Library of Congress Control Number: 2018951907

© Springer Nature Switzerland AG 2018

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, express or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature
Switzerland AG
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

We respectfully dedicate this volume to Prof. Michael Havey and Dr. Chris Kik for their work on Allium genome construction. Without their pioneer spirit the Allium research community could not have launched DNA marker breeding and whole genome sequencing.



With respect to the photo:

From left to right: Dr. E.R.J. Keller, Dr. G. Galvan, Prof. M. Shigyo, Dr. O.E. Scholten, Prof. M. Havey, Dr. A.W. van Heusden, Dr. C. Kik.

The photo was taken in Dronten, the Netherlands on November 9 2007.

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 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 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, 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. 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 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 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, 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 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 to the Volume

The *Allium* vegetable crops including onion, garlic, leek and Japanese bunching onion are one of the earliest domesticated crops, that has been broadly cultivated and prized for its flavor, medicinal, and nutritional properties. The word “*Allium*” is derived from the Greek word also “ἀλόη” which means “to avoid”, because of its offensive smell. References to these plants in the Bible and the Quran reflect their importance to ancient civilizations both as flavorful foods and as healing herbs. Currently, bulb onion annual production was estimated to be approximately 93.16 million tons in 2016 according to FAOSTAT (accessed 2018), which ranked onion third after tomato and watermelon in the global vegetable crops. The rigorous estimation of the economic effect of these cash crops seems to be outside the bounds of possibility due to the traditional utilization of some minorities as an indigenous plant in the remote and backward village. Thus, *Allium* species have made a significant contribution toward our dietary life.

During domestication, the genomes of many crop species have become more complex, with increasing numbers of repetitive DNA sequences. For instance, the paleontological species such as bulb onion, bunching onion, garlic, etc., the transposon would be responsible for the enormity of genome size attributively together with a minor DNA restructuring by point mutation. Such a complicated genome reorganization is estimated to cause the speciation of *Allium*, which is the primary factor for reproductive isolation followed by the enlargement of habitat range and the creation of noble utilization forms in the species of this genus. Next-generation sequencing (NGS) technologies allow hundreds of thousands to billions of nucleotide reads, which help in understanding the genetics of complex traits and to provide insights into genomic variation, (single-nucleotide polymorphisms (SNPs), insertions/deletions (InDels) and other structure of variances (SVs)), quantitative trait locus (QTL) introgressions, and have facilitated the development of gene expression atlases and increased our understanding of the signaling pathways involved in the responses of plants to biotic and abiotic stressors. To proceed genome analysis of *A. cepa* and its functional study, *Allium* international research community have developed several types of artificially manipulated genetic stocks and applied these stocks to the latest modern analysis technology.

The present book entitled “*The Allium genomes*” aims to present a full picture of the state-of-the-art research and development of *Allium* vegetable

crops, including species and genetic resources, genetics and gene mapping, breeding and cytogenetics as well as taxonomical and ethnobotanical aspects. The 14 chapters represented in this book will provide the readers with the recent advances in *Allium* crop genomics, including (1) the economic and academic importance of *Allium* species such as onion, leek, garlic and Japanese bunching onion, (2) taxonomical and ethnobotanical aspects of *Allium* species from Middle Asia with particular reference to subgenus *Allium*, which could be of interest for innovative breeding concerning pharmaceutical, ornamental, and edible traits, (3) an update of *Allium* genetic resources, (4) the classical genetics of gene mapping for perspective onion breeding, (5) the molecular cytogenetic progress in the study of the *Allium* chromosomes and its applications in onion breeding, (6) the novel knowledge of cytoplasmic genomes, (7) cytogenetic aspects of repetitive sequences, (8) molecular genetics of simple sequence repeat, (9) theoretical description of gene annotation, (10) gene family evolution in *Allium* species, (11) strategies and tools for sequencing in structural and functional genomic resources, (12) the targeted and untargeted metabolomic profiling of bioactive metabolites in *Allium* crops, (13) Progress to date and development of new population resources for molecular mapping by NGS technology, (14) the clarification of the impact on *Allium* plant breeding along with the background history of the national and international genome initiatives. This book attempted to maximize the involvement and collaboration between *Allium* breeders and researchers all over the world to enhance the transfer of laboratory-based innovations to end-user practice for the improvement of *Allium* crops and food sustainability.

We are grateful to all our colleagues for their contribution. We wish to record our thanks and appreciations for Prof. Chittaranjan Kole, the Series Editor, for his assistance and guidance right from the inception till the publication of this book.

For our international research community on *Allium* genomics, the leadership of two scientific authorities in the last three decades will never be forgotten in everyone's mind. Dr. Michael Havey has been a USDA Research Geneticist and Professor in the Department of Horticulture at the University of Wisconsin–Madison since 1988. He had spent 30 years for his research on the breeding, genetics, and genomics of the Alliums (onion and garlic). Since 1988 at Wageningen, Dr. Chris Kik had been a senior researcher for 17 years in the Plant Research International (PRI) formerly known by the Centre for Plant Breeding and Reproduction Research (CPRO-DLO). The activity of his research group was intense along with a number of the EU projects including “Garlic & Health” during that time. Dr. Kik also organized several collecting missions for plant genetic resources as a head curator for crop plants in Centre for Genetic Resources, the Netherlands since 2005. Both of them are scientifically advanced and have high standards of practical research on pre-breeding or DNA marker breeding in *Allium*. Furthermore, both of global leaders, Dr. Havey and Dr. Kik have spent a lot of time for training of young scientists from different parts of the

world. In this book, most of the contributors consist of their favorite disciples in different countries. As shown in a previous page, we would like to dedicate this book to Prof. Michael Havey and Dr. Chris Kik with our great compliments.

Yamaguchi, Japan
New Delhi, India
Tottori, Japan

Masayoshi Shigyo
Anil Khar
Mostafa Abdelrahman

Contents

1	Economic and Academic Importance	1
	Claudio R. Galmarini	
2	Taxonomical and Ethnobotanical Aspects of <i>Allium</i> Species from Middle Asia with Particular Reference to Subgenus <i>Allium</i>	11
	Furkat O. Khassanov	
3	<i>Allium</i> Genetic Resources	23
	E. R. Joachim Keller and Chris Kik	
4	Classical Genetics on Gene Mapping	53
	Ali Fuat Gökçe	
5	Cytological Details of Genome	67
	Ludmila Khrustaleva	
6	Cytoplasmic Genome	89
	Mai Tsujimura and Toru Terachi	
7	Repetitive Sequences	99
	Maki Yamamoto	
8	Simple Sequence Repeat	113
	Hikaru Tsukazaki	
9	Gene Annotation	129
	Hideki Hirakawa	
10	Gene Family Evolution in <i>Allium</i> Species	145
	Jiffinvir Khosa, Robyn Lee, John McCallum and Richard Macknight	
11	Structural and Functional Genomic Resources Developed	161
	Go Suzuki, Turgut Yigit Akyol and Shusei Sato	
12	Metabolomics of <i>Allium</i> Crops	173
	Yuji Sawada	

13 Molecular Mapping of Genes and QTL: Progress to Date and Development of New Population Resources for NGS Genetics	181
John McCallum, Samantha Baldwin, Richard Macknight, Jiffinvir Khosa and Martin Shaw	
14 Impact of the <i>Allium</i> Genomes on Plant Breeding	197
Michael J. Havey	
15 Future Perspective	215
Mostafa Abdelrahman, Anil Khar and Masayoshi Shigyo	

Abbreviations

2-CPGTH	S-2-Carboxypropylglutathione
ABS	Access and Benefit Sharing
ACSOs	S-alk(en)yl-L-Cysteine Sulfoxides
AFLP	Amplified Fragment Length Polymorphism
AGL6	AGAMOUS LIKE6
AIRDC	Association of International Research and Development Centers
ALL1	Alliinase
AMOVA	Molecular Variance
ANS	Anthocyanidin Synthase
AOX	Alternative Oxidase
AP2	APETELLA 2
ATC	<i>Arabidopsis thaliana</i> Relatives of Centroradialis
ATP	Adenosine Triphosphate
AVRDC	Asian Vegetable Research and Development Center
BAC	Bacterial Artificial Chromosome
C	Color Factor
CAN-ABS	Competent National Authority on ABS
CBD	Convention on Biodiversity
CGIAR	Consultative Group on International Agricultural Research
CgMS	Cytoplasmic-Genic Male Sterility
CGN	Centre for Genetic Resources, the Netherlands
CHI	Chalcone Isomerase
ChIP	Chromatin Immuno Precipitation
CHS	Chalcone Synthase
cM	Centi-Morgans
CMS	Cytoplasmic Male Sterility
CO	CONSTANS
DDA	Data-Dependent Analysis

DFR	Dihydroflavonol 4-Reductase
DH	Doubled-Haploid
DSC	Differential Scanning Calorimetry
EALLDB	European Allium Database
ECPGR	European Cooperative Programme for Plant Genetic Resources
ESF	European Science Foundation
EST	Expressed Sequence Tags
FAOSTAT	Food and Agriculture Organization Statistics
FISH	Fluorescence In Situ Hybridization
FKF1	Flavin-Binding, Kelch Repeat, F-Box1
FT	Flowering Locus T
GBIF	Global Biodiversity Information Facility
GBIS	Genebank Information System
GCLV	Garlic Common Latent Virus
GG-PRENC S	Gamma-Glutamyl-S-1-Propenyl-L-Cysteine Sulfoxide
GG-PRENC SO	Gamma-Glutamyl-S-1-Propenyl-L-Cysteine Sulfoxide
GI	GIGANTEA
GISH	Genomic In Situ Hybridization
GPAT2	Glycerol-3-Phosphate Acyltransferase 2
GRIN	Germplasm Resource Information Network
GSCC	Garlic and Shallot Core Collection
HMW	High Molecular Weight
HRP	Horse Radish Peroxidase
IBPGP	International Board of Plant Genetic Resources
IGS	Intergenic Spacer
InDel	Insertion/Deletion
IPGRI	International Plant Genetic Resources Institute
IPK	Institute für Pflanzengenetik und Kulturpflanzenforschung
IPNI	International Plant Names Index
IT-PGRFA	International Treaty on Plant Genetic Resources for Food and Agriculture
ITS	Internal Transcribed Spacer
LC-MS	Liquid Chromatography–Mass Spectrometry
LC-Qq-Q-MS	Liquid Chromatography–Tandem Quadrupole–Mass Spectrometry
LD	Long Day
LFS	Lachrymatory Factor Synthase
LFY	Leafy
LIMS	Laboratory Information Management Systems
LSC	Large Single-Copy

LYSV	Leek Yellow Stripe Virus
MALs	Alien Monosomic Addition Lines
MAT	Mutually Agreed Terms
MRR	Mitochondrial Retrograde Regulation
MS	Mass Spectrometry
MS/MS	Tandem Mass Spectrometry
MT	Mitochondrial
MTA	Material Transfer Agreement
N	Normal
NEP	Nucleus-Encoded RNA Polymerase
NGS	Next-Generation Sequencing
N-msms	Maintainer Line
NOR	Nucleolus Organizer Regions
OYDV	Onion Yellow Dwarf Virus
PCR	Polymerase Chain Reaction
PEBP	Phosphatidylethanolamine Binding Domain Proteins
PEP	Plastid-Encoded RNA Polymerase
PGR	Plant Genetic Resources
PI	PISTILLATA
PIC	Prior Informed Consent
PPR	Pentatricopeptide Repeat
PRENC SO	<i>trans</i> -S-1-Propenyl-L-Cysteine Sulfoxide
QTLs	Quantitative Trait Loci
QTOF-MS	Liquid Chromatography–Quadrupole Time of Flight–Mass Spectrometry
RAPD	Random Amplified Polymorphic DNA
Rf	Fertility Restoration
RFLP	Restriction Fragment Length Polymorphism
ROS	Reactive Oxygen Species
S	Sterile
SD	Short Day
SDR	Second Division Restitution
SGR	Structural Genomic Resources
SiR	Sulphite Reductase
SLV	Shallot Latent Virus
SNP	Single Nucleotide Polymorphisms
SPE3	SEPALLATA3
SRAP	Sequence-Related Amplified Polymorphism
SRM	Selected Reaction Monitoring
SSC	Small Single-Copy

SSR	Simple Sequence Repeat
TCA	Tricarboxylic Acid
TFL1	Terminal Flower Like 1
TSA	Transcriptome Shotgun Assembly
WIEWS	World Information and Early Warning System



Economic and Academic Importance

1

Claudio R. Galmarini

Abstract

Allium species have been cultivated for thousands of years for its therapeutic properties, religious significance, taste and aroma. Most of the cultivated crops evolved from wild relatives that grow in central Asia. Nowadays, *Alliums* are major vegetable crops cultivated worldwide. The most important crops of this family are onion, garlic, shallot, leek and Japanese bunching onions. Worldwide the consumption of these vegetable crops is increasing, one of the reasons is consumer awareness of the potential of these vegetables to enhance health, to improve welfare and reduce the risk of diseases. In this chapter, the economic importance of the principal edible *Alliums* is described, information is given about the academic contribution to the knowledge of *Allium* crops in recent years,

and also future challenges are mentioned, especially those related to plant breeding, genetics and genomics, that will contribute to increase yields, quality and to have a more sustainable production.

1.1 *Allium* Economic Importance

Allium vegetables are the fourth most abundant group of commercially produced nonleguminous vegetables after potatoes, cassava and tomatoes according to FAO (2017) statistics. Onion, garlic, Japanese bunching onion, shallot and leek are the most crucial edible *Allium* crops. Nevertheless, over 20 other *Allium* species have been consumed by humans (van der Meer 1997). There are also *Allium* species used for ornamental purposes, such as *Allium aflatunense*. Seed production of *Allium* crops is also an important economic activity. *Allium* vegetables gross production value for 2014 was US\$61,348 million (FAO 2017); about 70% of this value is for dry onion bulbs, 25% for garlic, 4% for green onions and shallots and 1% for leeks. The production of *Allium* crops, especially garlic and onion shows an important increase since 2000, in great part, this fact is explained by an increase in *per capita* consumption, one of the reasons may be that consumers are aware of the potential of these vegetables to enhance health and prevent chronic diseases.

C. R. Galmarini (✉)
Instituto Nacional de Tecnología Agropecuaria
(INTA), Estación Experimental Agropecuaria La
Consulta, CC8 (5567), La Consulta, Mendoza,
Argentina
e-mail: galmarini.claudio@inta.gob.ar

C. R. Galmarini
Consejo Nacional de Investigaciones Científicas y
Técnicas (CONICET), Buenos Aires, Argentina

C. R. Galmarini
Facultad de Ciencias Agrarias, Universidad Nacional
de Cuyo, Almirante Brown 500, M5528 AHB
Chacras de Coria, Luján, Mendoza, Argentina

1.2 Onion (*Allium cepa* L.)

Onion is the most important *Allium* vegetable crop. Nearly 88 million tons per annum are worldwide produced (Table 1.1). Bulb onions are produced in different latitudes, from subarctic regions to regions close to the equator, although they are best adapted to production in temperate and subtropical areas (Brewster 2008). Onion gross production value for 2014 was US \$42,743 million (FAO 2017). Due to the storage and transport facility of the crop, there is a significant international trade; about 20 million tons are traded annually (FAO 2017). Due to this global trade, and because of the many techniques for growing and storing onions for sale year-round, bulb onions are available throughout the year in most countries. The use of onion F₁ hybrids is increasing worldwide; this tendency reaches different kinds of onion germplasm, such as Granex, long-day storage and Spanish onions.

The leading producers are China (20,507,759 tons), followed by India (around 13,000,000 tons), United States of America, Egypt, Iran, Turkey, Pakistan, Brazil, Russia and Republic of Korea (Data for 2014, FAO 2017).

The leading exporters include The Netherlands, China, Mexico, India, USA, Egypt, Spain, New Zealand and Argentina. The main importers are USA, United Kingdom, Malaysia, Germany, Saudi Arabia, Japan, Canada, Czech Republic, Republic of Korea and Brazil. As an example, The Netherlands produces large quantities of long-storing, spring-sown, pungent onions which are exported between September and April,

mainly to Germany and UK. In a Mediterranean country, like Spain, crops are planted in autumn and harvested during spring and summer. In large countries, like the USA, the market is supplied year-round with onions from different regions within the country and from bulbs that come from Mexico or countries from the Southern Hemisphere. The main producing areas are Idaho-eastern Oregon, California, Washington, Georgia and Texas. Countries of the Southern Hemisphere like Australia, New Zealand, Argentina and Chile have an essential export market in Europe, especially Germany and UK, and also their production is sold in Asian countries, like Japan and Malaysia, and even in USA and Canada. In the case of South America, Argentina is a vital onion exporter to Brazil (Galmarini 2001).

Onion prices tend to fluctuate widely from year to year making onion production a risky business. Since there is a global market in onion bulbs, there is little that producers in any one region can do to control the market and stabilize prices. One strategy is to add value to the production or produce particular products. An example of the latter is the sweet onion market. The production of this type of onions is very well developed in the United States, especially in Georgia and Texas. Moreover, in countries like Peru and Chile, sweet onions are produced to export to the United States market from January to May.

About 1% of the world onion cropped area is produced for the dehydration industry; nevertheless, this is an essential activity for

Table 1.1 World onion cultivated area, production, yield and consumption from 1970 to 2014

Year	Area (ha)	Production (tons)	Yield (kg/ha)	Consumption (kg/capita/year)
1970	1,334,693	16,748,643	12,549	4.15
1980	1,616,802	22,400,015	13,854	4.63
1990	1,885,700	30,609,791	16,228	5.29
2000	2,838,022	49,966,784	17,606	7.46
2010	4,174,459	78,984,889	18,921	10.53
2014	5,298,873	88,475,089	16,679	10.97

Source FAOSTAT (2017)

diversification. The production is concentrated in China, USA, India and Mexico in the Northern Hemisphere and in Argentina in the Southern Hemisphere. The industry uses cultivars that have high solids and pungent white bulbs.

Onion dry bulb production has increased through the years, mainly due to an increase in yields and the cropped area. The world average yield is about 16 t ha⁻¹. Nevertheless, there are growers that harvest more than 100 tons per hectare, due to good growing conditions, irrigation and excellent agronomic practices.

Since 1970, onion consumption has increased almost three times (Table 1.1). The average consumption is around 10 kg/capita/year, nevertheless in countries like Greece, Albania, Iran, Kuwait, Uzbekistan, and yearly onion consumption per capita is over 20 kg (FAO 2017). One reason for consumption increase may be the health-benefits that this vegetable brings to humans. The beneficial health-effects attributed to onions are essential for consumers and breeders (Galmarini 2010). Onion consumption has been associated with decreased cardiovascular events, because of their hypocholesterolemic, hypolipidemic, anti-hypertensive, antidiabetic, antithrombotic and anti-hyperhomocysteinemia effects, as well as with many other biological activities including antimicrobial, antioxidant, anticarcinogenic, antimutagenic, antiasthmatic, immunomodulatory and prebiotic activity (Corzo-Martinez et al. 2007). Garlic and onion have phytochemicals categorized as functional foods; some of them are fructans, flavonoids and organo-sulphur compounds (Galmarini et al. 2001).

Onion seed market is also important, around 50,000 tons are yearly produced (FAO 2017). Onion represents an important percentage of the total vegetable seed economic value commercialized in the world. Onion seed production is performed both in the Northern and Southern hemispheres. The main producing countries are the USA, The Netherlands, Japan, Turkey, China, Spain, Italy, France, Australia, Chile, Argentina and South Africa.

1.3 Garlic (*Allium sativum* L.)

Garlic is the second most widely cultivated *Allium* with a current worldwide production of 24.9 million tons per annum, cultivated in 1.5 million hectares (FAO 2017). Garlic gross production value for 2014 was US\$15,129 million (FAO 2017). Since 1970, world garlic production has increased more than 10 times, while cultivated area increased around four times, indicating an increment in yield (Table 1.2). In addition to fresh consumption, the production of dried and processed garlic products for use in the food industry and as dietary health food supplements is an important activity.

Garlic is mainly grown in temperate areas. The garlic bulb is well adapted to storage and transportation, and there is an important international trade. The main producing and exporting country is China, which produces around 80% of the total world production. Garlic output in China exceeded the figures recorded by the world's second-largest producer, India, more than tenfold. Other important producers are South Korea, Egypt, Russia, Myanmar, Spain, USA, Uzbekistan, Argentina and Brazil. The leading exporters are China, Spain, and Argentina, while the leading importers are Indonesia, Brazil, Vietnam, Syria, USA, Pakistan, Russia, Germany, Italy and France (FAO 2017). China dominates the fresh and dehydrated garlic international market, being the leading exporter.

According to FAO (2017), the world average yield is about 16 t ha⁻¹ of dry garlic; although there are countries with an average yield over 30 t ha⁻¹, due to good growing conditions, irrigation and excellent agronomic practices. Although garlic production history shows a steady increase during the past 45 years, the most dramatic increase in total production and yield has been observed in the past 15 years; the increase in yields of garlic produced in China is in great part responsible of this change.

Regarding consumption, in some countries like the Republic of Korea 10 kg/capita/year