

Compendium of Plant Genomes
Series Editor: Chittaranjan Kole

Ezio Portis
Alberto Acquadro
Sergio Lanteri *Editors*

The Globe Artichoke Genome

 Springer

Compendium of Plant Genomes

Series Editor

Chittaranjan Kole, Raja Ramanna Fellow, Government of India,
ICAR-National Research Center on Plant Biotechnology, Pusa,
New Delhi, 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 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.

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

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Ezio Portis · Alberto Acquadro ·
Sergio Lanteri
Editors

The Globe Artichoke Genome

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Editors

Ezio Portis
DISAFA Plant Genetics and Breeding
University of Torino
Largo P. Braccini 2
Grugliasco, Torino 10095
Italy

Alberto Acquadro
DISAFA Plant Genetics and Breeding
University of Torino
Largo P. Braccini 2
Grugliasco, Torino 10095
Italy

Sergio Lanteri
DISAFA Plant Genetics and Breeding
University of Torino
Largo P. Braccini 2
Grugliasco, Torino 10095
Italy

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

Chittaranjan Kole

Preface to the Series

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

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

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

Thus, the evolution of the concepts, strategies, and tools of sequencing and bioinformatics reinforced the subject of genomics—structural and functional. Today, genome sequencing has 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 of different generations facilitated this genome sequencing. At the same time, newer concepts and strategies were emerging to handle sequencing of the complex genomes, particularly the polyploids.

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

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

As I write this preface for the first volume of the new series “Compendium of Plant Genomes,” a net search tells me that complete or nearly complete whole-genome sequencing of 45 crop plants, 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 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 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

The globe artichoke (*Cynara cardunculus* var. *scolymus*), together with cultivated cardoon (*C. cardunculus* var. *altilis*) was domesticated in the Mediterranean region from the wild cardoon (*C. cardunculus* var. *sylvestris*). The species is a member of the *Compositae* (a.k.a. *Asteraceae*), which is the largest and one of the most ecologically successful botanical families, including species of great economic importance such as sunflower, lettuce and chicory. Italy, is the top globe artichoke producing country and harbours its richest primary gene pool, while Sicily Island is considered the place where globe artichoke domestication occurred. Over time, globe artichoke cultivation has spread to other Mediterranean countries and more recently to the Americas and China. The primary product of globe artichoke is the immature inflorescence, but, as well as other members of the *C. cardunculus* complex, it is a multi-use crop exploitable also a source of phenolics, sesquiterpene lactones and inulin as well as for the production of lignocellulosic biomass and seed oil for both edible and biofuel purposes.

In this book emphasis is given to the recent development of the globe artichoke and cultivated cardoon genome sequences, made available to the scientific community by a Consortium including two Italian Universities, namely the University of Torino (DISAFA) and the University of Catania (Di3A) in collaboration with the Genome Center of Davis (USA). The availability of globe artichoke genome sequence has already made it possible to deepen the knowledge on the structure and function of its genome organization, to perform the resequencing of genotypes of globe artichoke varietal types, in order to dissect the path from sequence variation to phenotype, as well as to accomplish comparative genomic studies within the *Compositae* family. Furthermore, has laid the groundwork for future genomic assisted breeding programs and the application of genome manipulation technologies.

This book also provides exhaustive information on *C. cardunculus* botany, domestication, propagation, genetic resources, uses and pathways involved in the synthesis of bioactive compounds. Moreover, it includes a survey of the state of the art on the development of genetic maps and location of genes and QTLs affecting traits of economic interest.

Torino, Italy

Ezio Portis
Alberto Acquadro
Sergio Lanteri

Contents

1	<i>Cynara cardunculus</i> L.: Historical and Economic Importance, Botanical Descriptions, Genetic Resources and Traditional Uses	1
	Gaetano Roberto Pesce and Giovanni Mauromicale	
2	<i>Cynara cardunculus</i> Propagation	21
	Nicola Calabrese, Vanina Cravero and Mario A. Pagnotta	
3	Globe Artichoke Tissue Culture and Its Biotechnological Application	41
	Cinzia Comino, Andrea Moglia, Annamaria Repetto and Raffaella Tavazza	
4	<i>Cynara cardunculus</i> as a Multiuse Crop	65
	Giovanni Mauromicale, Gaetano Roberto Pesce, Maria Dolores Curt, Jesús Fernández, Javier González, Jorge Gominho, Rafael Tabla, Isidro Roa and Ezio Portis	
5	Bio-active Compounds and Their Synthetic Pathway	99
	Vincenzo Lattanzio, Cinzia Comino, Andrea Moglia and Sergio Lanteri	
6	Genetics and Breeding	115
	Ezio Portis, Alberto Acquadro and Sergio Lanteri	
7	Insights into the Population Structure and Association Mapping in Globe Artichoke	129
	Domenico Rau, Monica Rodriguez, Giovanna Attene, Limbo Baghino, Anna Barbara Pisanu, Davide Sanna, Alberto Acquadro, Ezio Portis and Cinzia Comino	
8	Cytological and Molecular Cytogenetic Insights into the <i>Cynara cardunculus</i> Genome	145
	Debora Giorgi, Gianmarco Pandozy, Anna Farina, Valentina Grosso, Paola Crinò and Sergio Lucretti	
9	Genomics	163
	Davide Scaglione, Alberto Acquadro, Ezio Portis and Sergio Lanteri	
10	The Chloroplast Genome	185
	Gabriella Sonnante	

11	miRNome	195
	Lorenzo Barchi and Alberto Acquadro	
12	Genome Resequencing	205
	Alberto Acquadro, Lorenzo Barchi, Ezio Portis and Sergio Lanteri	
13	Genome Database (www.artichokegenome.unito.it)	219
	Ezio Portis, Flavio Portis, Luisa Valente, Lorenzo Barchi, Sergio Lanteri and Alberto Acquadro	
14	Future Prospects	231
	Alberto Acquadro, Ezio Portis and Sergio Lanteri	

Cynara cardunculus L.: Historical and Economic Importance, Botanical Descriptions, Genetic Resources and Traditional Uses

Gaetano Roberto Pesce and Giovanni Mauromicale

Abstract

The chapter begins with a brief etymological discussion, followed by an overview of ancient sources that speak of *Cynara cardunculus*. According to these testimonies, the domestication of the globe artichoke could have begun in the first century CE. Then the most recent statistics on globe artichoke in the world are explained; they show that, in recent years, its cultivation is spreading even in countries that are not traditionally producers. The chapter also provides the botanical classification and the description of the species, highlighting that three botanical varieties are distinguishable, namely globe artichoke, cultivated cardoon and wild cardoon. The latter is thought to be the progenitor of both the cultivated forms. There is also a remarkable diversity of forms and cultivars of globe artichoke and cardoon, as explained in the paragraph about genetic resources. The chapter ends with a description of the traditional uses of globe artichoke and cardoon.

1.1 Historical Outline, Spread in the World and Economic Importance

The English name «artichoke» derives from northern Italian «articiocco» (Skeat 1887), which in turn derives, like the Spanish «alcachofa», the Portuguese «alcachofra» and the Italian «carciofo», from the Arabic خرشوف (kharshuf) through the Hispanic Arabic «al-harsúf». The adjective ‘globe’ refers to immature inflorescence (head, capitulum) with the appearance of a pine cone and a globe shape, to distinguish it from two other vegetables, named artichoke: Jerusalem artichoke (*Helianthus tuberosus* L.) and Chinese artichoke (*Stachys sieboldii* Miq.) grown for their edible stem tubers. The genus name *Cynara* could derive from the Greek κῦων (kyon—dog) (Craig 1858). The reference to the dog has a negative connotation, because of the objectionable thorns, which are likened to a dog’s teeth (Small 2009). The name *Cynara* could be also related to Κινάρος (Kinaros), an island of Aegean Sea, for a kind of globe artichoke native to that island (Quattrocchi 1999). However, as we shall see, the word κινάρα (kinara), less frequently κυνάρα (kynara), is found in literature to probably indicate the globe artichoke. The specific epithet *cardunculus* comes from Latin *carduus* with diminutive suffix *-unculus*, namely little cardoon. *Scolymus*, namely the former specific epithet of globe artichoke and its current botanical variety,

G. R. Pesce · G. Mauromicale (✉)
Di3A (Dipartimento di Agricoltura, Alimentazione e Ambiente), University of Catania, via Valdisavoia 5, 95123 Catania, Italy
e-mail: g.mauromicale@unict.it

is the latinization of σκόλυμος (scolymos), which belongs to the semantic field of ‘thorn’ (σκόλοψ—scolops). On this, Hesiod (eighth–seventh century BCE), in his ‘Works and Days’, and Theophrastus (fourth–third century BCE), in his ‘Enquiry into Plants’, used the word σκόλυμος to refer to *Scolymus hispanicus* L. (Liddell and Scott 1996). Again in the cited work, Theophrastus referred to a plant calling it κάκτος (kaktos), maybe the cardoon, and stated that it only grows in Sicily and not in Greece. But if we take a leap forward by a few centuries, we read that Athenaeus (second–third century CE) in his ‘Deipnosophists’ challenged Theophrastus. He was indeed sure that κάκτος (kaktos) was what the κινάρα (kinara) was for the Greeks. He also stated that the plant called κάκτος (kaktos) is the same plant that the Romans called κάρδος (cardos, *carduus* in Latin). After all, Athenaeus wrote, κάκτος (kaktos) and κάρδος (cardos) differ only by two letters. Consequently, Athenaeus made no difference between κινάρα (kinara) and *carduus*. From this overview, a certain vagueness emerges in the ancient references, and for this reason De Candolle (1885) suggested that cultivated globe artichoke was unknown in classical times. However, Columella (first century CE) in his ‘On Agriculture’ talked about *cinara*, defining it *hispidus* (spiny), and was the first to provide a description of what is probably the globe artichoke, for at least two reasons. The first is the fact that he focused his attention on the capitulum. The second is that he spoke about cultivation practices that seem more suited to the globe artichoke than to the wild cardoon. He also wrote about making cheese using the wild cardoon flower (*agrestis cardui flore*) as rennet. In Chap. 43 of book XIX of his ‘The Natural History’, Pliny the Elder (first century CE) wrote about *carduus*, cultivated in Carthage and especially in Cordoba (*apud Carthaginem Magnam Cordubamque praecipue*). He also wrote that this crop is very profitable, although he did not understand why it was so appreciated; in fact, he thought that it was a monstrosity that not even beasts would eat. According to Foury (2005), Pliny was speaking of the globe artichoke. Indeed, the use of the word ‘monstrosity’ could

derive from the wonder in front of a novelty represented by the large capitulum. A little further on (book XXI, Chap. 59), Pliny wrote about the *cactos*, clearly copying what Theophrastus had written. Foury (1989) deduced, based on Columella and Pliny’s writings, that the cultivation of globe artichoke started around the first century CE. Probably in the same period, the domestication of globe artichoke was ongoing, but not accomplished (Sonnante et al. 2007b). In this regard, Sicily is supposed to be one of the centres of domestication of the globe artichoke (Mauro et al. 2009). Pedanius Dioscorides (first century CE), who was a physician, pharmacologist and botanist, in his ‘On Medical Material’, gave just a quick nod to κινάρα (kinara), but Galen (second century CE), in his ‘On the power of foods’, spoke more widely about the globe artichoke, pointing out that some call it κινάρα (kinara) and others κυνάρα (kynara), blaming the latter as a solecism. He also noted that many people consumed the plant’s capitulum, which they called ‘vertebra’ [σφόνδυλος/σπόνδυλος (sfondylos/spondylos)]. The word ‘vertebra’ to refer to the capitulum also appears in the Diocletian’s Edict on Maximum Prices of 301 CE, both in Greek and in Latin [σφόνδυλοι κιναρῶν (sfondyloi kinaron), *sponduli*]. In the third or perhaps fourth century CE, a compilation of recipes under the name of Apicius, ‘On the Subject of Cooking’, was compiled. It contains three recipes for cardoons (*cardui*) and seven recipes for *funduli* or *sfondili*, which are, according to Foury (2005), receptacles. Some Roman mosaics conserved in the Bardo Museum in Tunis datable to the Imperial period (second and third century CE) show heads of globe artichokes (both spiny and spineless) (Fig. 1.1). We have little knowledge about globe artichoke in the Middle Ages, because of a surprising historical-documentary eclipse. After the fall of the Western Roman Empire (end of the fifth century), the Eastern Roman Empire continued to prosper and expand; there, vegetables were in great demand and their cultivation spread outside the city walls from the second half of sixth century (Foury 2005). Chapter 39 of XII book of ‘Geoponica’ (tenth century) speaks about the

cultivation of κινάρα (kinara). Among other things, the chapter contains some curious tips on how to get tasty ‘fruits’ (capitula); it is attributed to Marcus Terentius Varro, although you cannot find it in his ‘Agricultural Topics in Three Books’. After the Umayyads conquered the Iberian Peninsula (eight century), agriculture improved from a technological point of view and was enriched with the introduction of new cultivated species. This would reasonably suggest that the cultivation of the globe artichoke was maintained in those territories, as a legacy of the Roman Empire, and that it was not introduced from the East (Foury 2005). In paragraph 658 of ‘Compendium on Simple Medicaments and Foods’, Ibn al-Baitar (first half of the thirteenth century), described a plant called «harshef», which actually includes two forms: one wild and the other cultivated. The latter, called «kenguer» or «kenarya» in Andalusian, is described in paragraph 1976 of the same work. Clearly, it is hard to miss the similarity between the Andalusian «kenarya» on the one hand and the Latin *cinara* or the Greek κινάρα (kinara) on the other. According to Foury (2005), it is quite probable that the *cinara* described by Columella, and therefore our globe artichoke, survived in the Hispanic–Berber refuge until the fifteenth century. The technical skill of the Andalusian

agronomists and gardeners has probably led to the improvement and diversification of the globe artichoke, above all through the propagation by seed frequently used at the time. Mauro et al. (2009) hypothesize that globe artichoke was selected to become the plant we know today in the domestic vegetable gardens and in the monasteries, in the period between the ninth and sixteenth centuries. Around 1466, on the threshold of the Modern Age, globe artichokes had been transported from Naples to Florence, from where, according to Jean Ruel, they passed to France at the beginning of the sixteenth century. Hermolao Barbaro says that in 1473, in Venice, globe artichoke appeared as a novelty. In the early Modern Age (sixteenth century), globe artichoke spread in Europe, as witnessed by paintings not only from Italy, but also from Flanders and Bohemia (Fig. 1.2).

The most recent statistics on globe artichoke in the world show that the most important producer country is Italy (Fig. 1.3) with almost 44,000 ha and $\sim 406,000$ t year⁻¹. Italy alone accounts for about 27% of the world production (FAOSTAT 2018). Traditionally, globe artichoke is cultivated in Mediterranean countries, where it is almost 80% of the world’s globe artichoke growing areas, with nearly three-quarters share of the output (Fig. 1.3), but other countries—



Fig. 1.1 Roman mosaics depicting globe artichokes (second and third centuries). Bardo National Museum, Tunis



Fig. 1.2 Giuseppe Arcimboldo, ‘Vertumnus’ (1590–1591). This painting portrays Emperor Rudolf II of Habsburg as Vertumnus, a Roman deity (circled in red, a globe artichoke). It is kept in Skokloster Castle in Häbo, Sweden

especially Peru, Argentina and China—produce significant amounts (FAOSTAT 2018). In this regard, Fig. 1.4 provides the charts of globe artichoke production in the current main producing countries. These charts just give us an idea of the production trends in the period from 1961 to 2016 (FAOSTAT 2018). It is noticeable

that traditionally producing countries, such as France, Greece, Spain and even Italy, have a decreasing trend, while other countries, among which Egypt stands out, have increased their production in the last few years. In the same way, it should be noted that even countries outside the Mediterranean basin (such as Argentina, China and Peru) are increasing their production. In general, it can be said that even if the globe artichoke is still mainly produced in the countries of the Mediterranean basin, it is slowly spreading in the rest of the world. Bianco (2012) has summed up this situation aptly: ‘Artichoke: an international soul, but a Mediterranean heart’. The FAO (2018) also provides data on the globe artichoke trade, which however are largely indicative. Figure 1.5 represents the main commercial flows of the globe artichoke; the values shown are the averages of the three-year period (2014–2016). In order to represent the most significant trade movements, only flows greater than US\$500,000 were taken into consideration. Figure 1.5 clearly shows that France is the main importing country, Spain being the main exporting country. The most important trade flow is between these last two countries, more precisely from Spain to France. Spain is almost a net exporter (it imports very little product), while France and Italy are at the centre of a dense network of imports and exports. The figure also shows that globe artichoke exchanges in the American continent are separate from the rest of

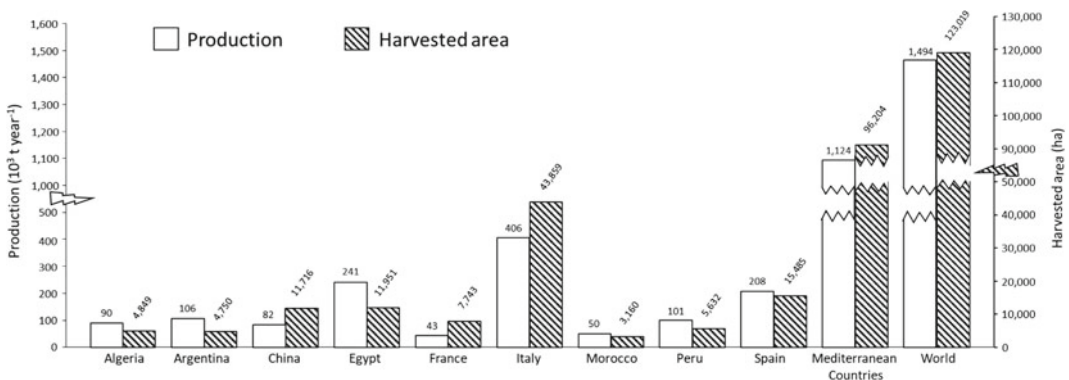
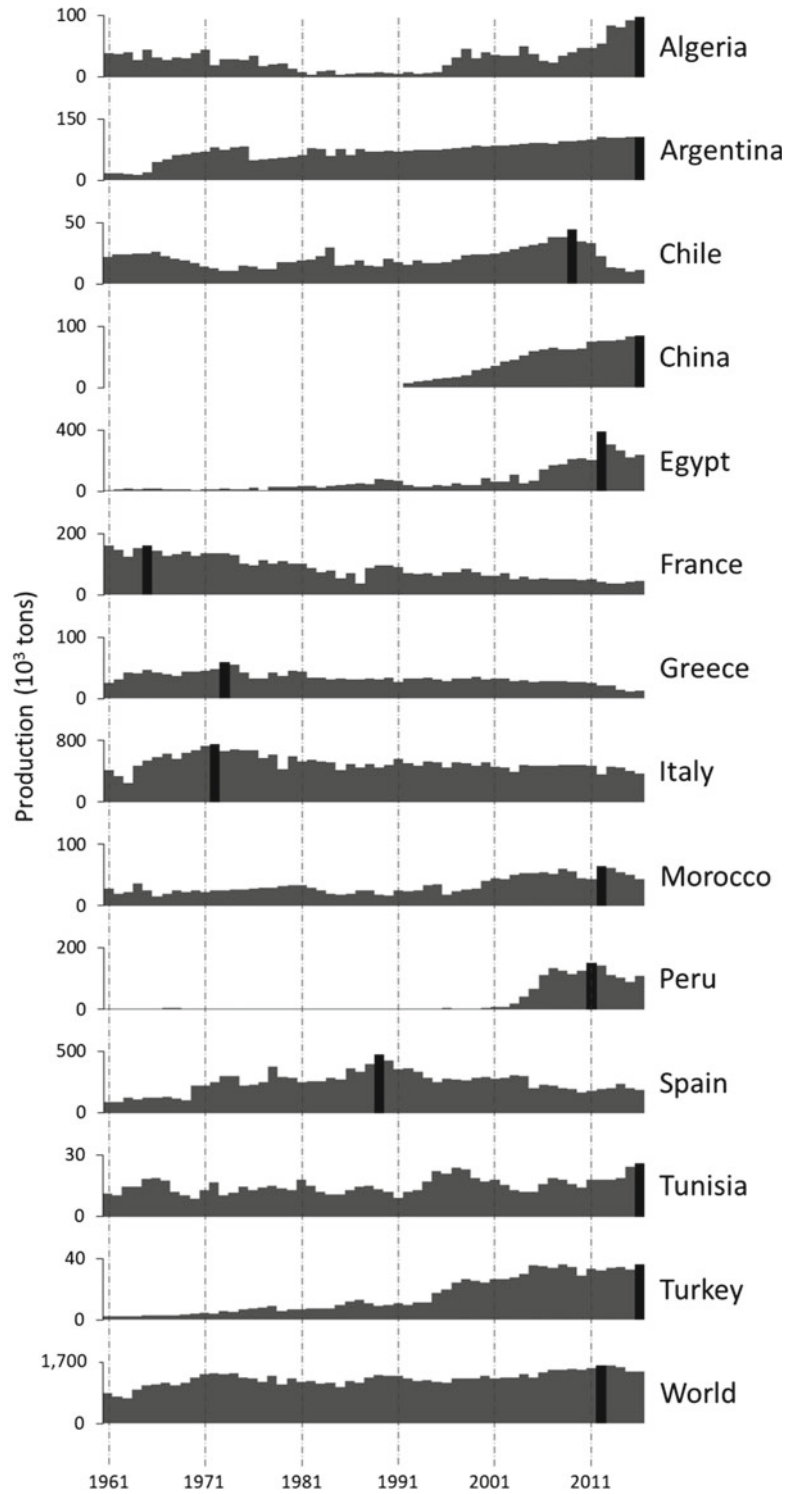


Fig. 1.3 Globe artichoke annual production and harvested areas in the main producing countries. Considered period 2014–2016. Source FAOSTAT (2018)

Fig. 1.4 Charts of globe artichoke production in the main producing countries. In each chart, the year of greatest production is coloured in black. Considered period 1961–2016. *Source* FAOSTAT (2018)



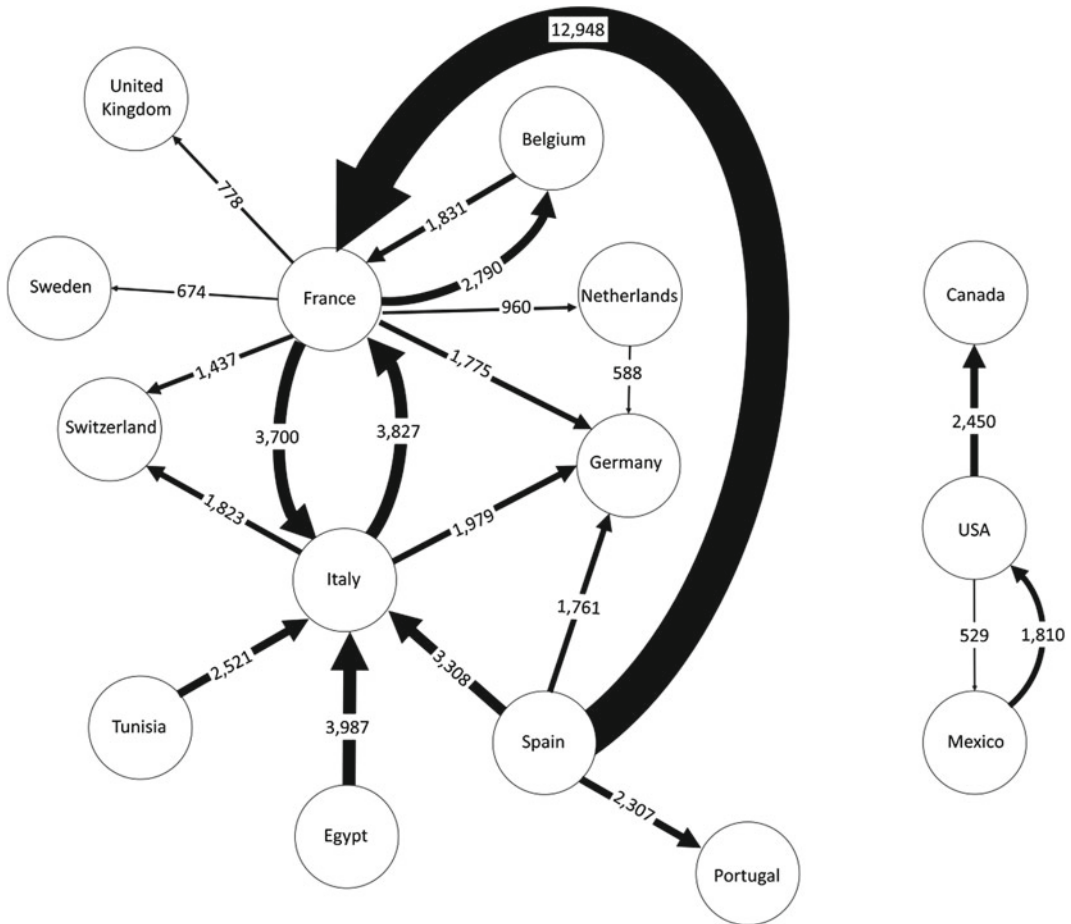


Fig. 1.5 Diagram of main trade flows of globe artichoke in the world (only flows exceeding \$500,000 are considered). Values are expressed as thousands of US dollars,

and the width of the arrows corresponds to the size of the flows. Considered period 2014–2016. *Source* FAOSTAT (2018)

the world, or at least the significant ones as defined above. This diagram does not include Algeria, Argentina, China, Morocco and Peru, which are among the major producer countries; they allocate their production mainly to domestic consumption or, in some cases, their exports are not taken into account by official sources. The comparison between Figs. 1.6 and 1.7 shows the variation of the gross production values of globe artichoke in the different continents over a period of twenty years (between 1994–96 and 2014–16). The total value does not change very much (from 1058 to 991 million US dollars), while it is

clear that the hub of production moves a little from Europe to the other continents. In fact, the gross production value of Europe has decreased by 6%, while those of Africa, Americas and Asia have increased respectively by 252, 52 and 134%.

Regarding the cartoon, unfortunately there is not the same abundance of official statistics as for the globe artichoke. The areas devoted to cartoon cultivation (officially about 2–3000 ha, though this value is underestimated) are localized in Spain, Italy, France and Greece (Ierna and Mauromicale 2010).

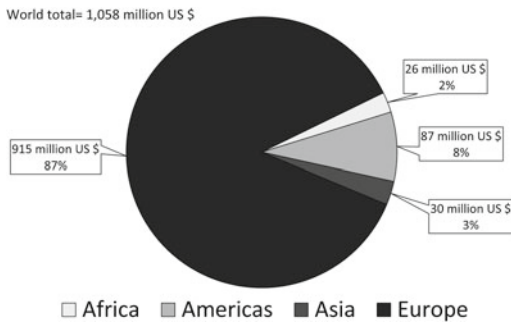


Fig. 1.6 Gross production values of globe artichoke expressed as constant 2004–2006 million US dollars in the different continents. Considered period 1994–1996. Source FAOSTAT (2018)

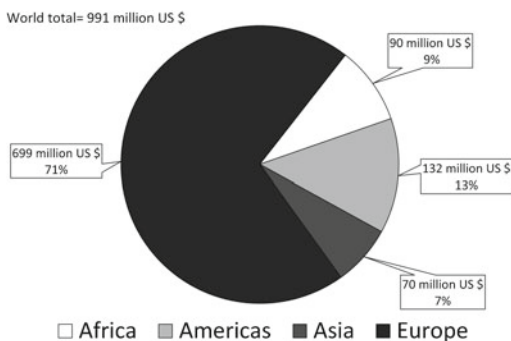


Fig. 1.7 Gross production values of globe artichoke expressed as constant 2004–2006 million US dollars in the different continents. Considered period 2014–2016. Source FAOSTAT (2018)

1.2 Botanical Classification and Description of the Species

The genus *Cynara*, belonging to the Asteraceae family, is native to the Mediterranean region, sharing its distribution with the olive (*Olea europaea*). The members of the genus are the *Cynara cardunculus* L. species complex, consisting of the globe artichoke [var. *scolymus* (L.) Fiori], the cultivated cardoon (var. *atilis* DC.) and the wild cardoon [var. *sylvestris* (Lamk) Fiori], and other six wild species. The three *C. cardunculus* forms are fully cross-compatible with one another, and form fertile intervarietal hybrids (Basnizki and Zohary 1994). The predominant allogamy of *C. cardunculus* led to the

formation of populations whose kinship is difficult to understand. Studies on the isoenzymatic relationships (Rottemberg et al. 1996), the intercross (Rottemberg and Zohary 1996), as well as on genetic and molecular relationships intra- and intervarietal (Lanteri et al. 2004a, b; Portis et al. 2005a, b, c; Mauro et al. 2009) lead to the conclusion that the cultivated botanical varieties of *C. cardunculus* L. are phylogenetically very close to the wild cardoon, which is probably the common ancestor of the first two. Presumably, from the latter species two divergent lines were implemented: one selected for the width of the leaf midrib, leading to the cultivated cardoon, the other for the head size, leading to the globe artichoke (Basnizki and Zohary 1994; Lanteri et al. 2004b).

1.2.1 Globe Artichoke

Globe artichoke (Figs. 1.8 and 1.9) is a perennial herbaceous plant that can be reproduced by achenes (improperly called ‘seeds’) or usually vegetatively propagated by side offshoots originating from underground buds, *ovoli* (underground semi-dormant dried offshoots with apical and lateral buds) or by division of rooted basal stem portions. Tissue culture procedures are occasionally used for nursery production of disease-free plantlets. However, these in vitro multiplication methods have not yet been optimized, and success is still poor, at least for early Mediterranean genotypes such as ‘Violet de Provence’, ‘Violetto di Sicilia’ and ‘Blanca de España’. Plants, when grown from achenes, have a primary taproot and numerous adventitious secondary roots, whereas plants from offshoots, *ovoli* or other vegetative parts have fibrous adventitious roots that enlarge over time (while the smallest disappear), losing their absorption function in order to become storage organs and provide support (Bianco 1990). Their total depth is about 40 cm. While the plant grows, a rhizomatous stem, commonly called *ceppaia* in Italian, becomes increasingly evident at the base of the main stem, and on its surface several buds differentiate, originating offshoots. Offshoots do

not all develop at the same time, but in sequence because of apical dominance, hence on the same *ceppaia* buds at different age and physiological stage are usually present. Apical dominance intensity varies depending on the cultivar (Mauromicale and Copani 1990) and decreases when the main shoot differentiates the main head. The latest offshoots, which did not produce heads, dry up their aboveground fraction at the onset of summer drought, becoming *ovoli* (Jannaccone 1967). During the vegetative phase, the caule is very short, so the plant has some whorls of leaves, clustered tightly at its base, giving it a typical ‘rosette’ form. Leaf size, shape and number are variable depending on the cultivar and phenological growth stages. They are ashy green coloured on the lower side, have thick midribs and are typically fewer in the earliest cultivars. The apical bud of each shoot switches from the vegetative phase to reproductive phase. The flower stem, variable in length depending on the cultivar, on the time of year and on eventually supplied hormone treatments, is cylindrical, ashy green coloured, longitudinally ribbed, erect and has ramifications that vary in number. It has trichomes and alternate lanceolate leaves. Stems of first, second, third (and so on) orders also have a capitulum at their distal end, whose size decreases as the order of ramification increases. The plant, depending on the cultivar, may produce from 3–4 to 20 capitula. The weight of a single capitulum can vary greatly depending on the cultivar and its position in the plant, but in general it can be said to range between 100 and 300 g. In most cultivars, a well-developed capitulum contains from 800 to 1400 florets (Bazniski and Zohary 1994). The latter are hermaphrodite, tubular, proterandrous and blue-violet coloured. The fruit is a tetragon-shaped or flattened cypsela or achene, dark-coloured or greyish, uniform or mottled, whose weight ranges between 30 and 70 mg. The calyx, metamorphosed into a feathery organ (pappus), favours dissemination. Commonly the two terms ‘cypsela’ and ‘achene’ are used interchangeably; however, in the course of this chapter, the term ‘achene’ is used. The three botanical varieties of *C. cardunculus* have the

same floral biology, as explained later in the paragraph on the cultivated cardoon. Since the main product of the globe artichoke is the capitulum, it is worthwhile dwelling on the flowering transition of the vegetative apex. In this regard, Morone Fortunato et al. (1981) made microscopic observations during the formation of the capitulum on four cultivars of globe artichoke. The vegetative apex of the globe artichoke (Fig. 1.10) is formed by a *tunica*, with 8–9 cell layers, and a less homogeneous *corpus* than the *tunica*. The *tunica* is made up of two parts: one is the central apex, consisting of two initial cells recognizable because of their greater diameter. The other is located between the initial cells and the primordia of the leaves. This part is made up of smaller cells that divide more frequently.

The corpus instead is divided into three zones:

- (a) the zone of the mother cells, which represent the initial cells of the corpus, located under the initial cells of the *tunica*;
- (b) the rib-meristem, consisting of the cells arranged in columns. They are larger the further they are from the apex; in this zone, the divisions generally occur according to a plane perpendicular to the axis of the apex;
- (c) the flank-meristem, consisting of cells that envelop the rib-meristem, this zone contributes to the development of the leaves primordia and procambium.

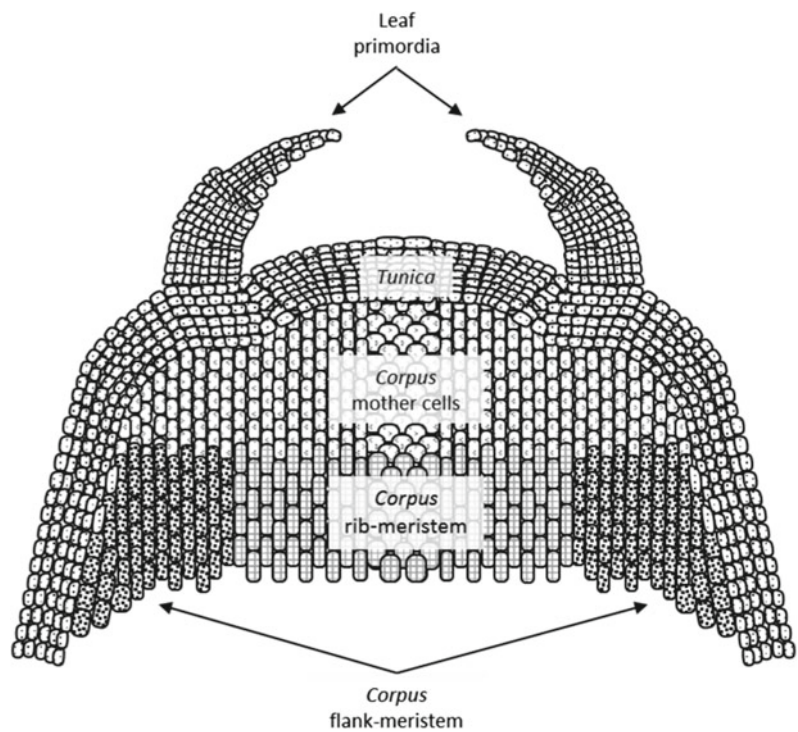


Fig. 1.8 Globe artichoke field (photograph taken by Mauromicale)



Fig. 1.9 Biodiversity in globe artichoke (photograph taken by Mauromicale)

Fig. 1.10 Schematic representation of globe artichoke vegetative apex according to Morone Fortunato et al. (1981)



The meristematic apex in the vegetative phase appears as a small dome set within the hood of the young leaves. In the very early stages of the

reproductive transition, there is an increase in mitotic activity at the border between the central area of the mother cells and the rib-meristem.

Gradually, this activity expands in the central zone of the mother cells, where the cells become small and rich in protoplasm. The mitotic activity does not appear in the cells of the rib-meristem and in the underlying pith. Therefore, the apex has a parenchymatous pith, surrounded by some layers of meristematic cells that gradually decrease to form a mantle–core structure (this is the reproductive transition). The apex, which was previously globose, flattens and expands progressively, highlighting the mantle formed by the two meristematic layers, which overlap the parenchymatous heart. In this stage, on the peripheral area of the apex surface, the flower primordia make their appearance and develop in a centripetal sense. When the florets have developed on the whole thalamus, then the differentiation is complete.

Macroscopically, the flower organogenesis of the head of the cultivar Violet de Provence is shown schematically through the following sequence of phenological stages (Foury 1967):

R: indicates the caulinar apex transition from the vegetative phase to the reproductive one;

A: the head is perceptible to the touch but it is completely enveloped in a leaf rosette that surrounds the caulinar structure;

B: the lengthening of the stem and the deployment of the leaves allow seeing the head at the centre of the leaf rosette;

C: the head is fully visible, and the inflorescence reaches a length of 2–4 mm;

D: the flower stem is fully stretched, and head has reached the optimum size for harvesting;

E: external bracts begin to diverge and the thalamus, which was concave, begins to flatten, while central flowers (florets) reach a length of about 2 cm;

F: the central bracts open, and in the centre the first florets appear;

G: appearance of the flowers and anthesis of peripheral flowers.

Baggio et al. (2011) describe 15 development scale stages of ‘Nobre-UPF’, a Brazilian cultivar. Seven of them are equivalent to the first observed by Foury (1967), while the other eight stages

comprise the phases from the full-opening of the capitulum to the fruit dispersion.

1.2.2 Cultivated Cardoon

Commonly known as cynara, cardoon is a perennial (~10 years) field crop for numerous purposes and non-conventional use (Gominho et al. 2018). It is well adapted to the xerothermic conditions of southern Europe. The cardoon has an annual development cycle, in which the plants grow and develop during autumn, winter and spring, with summer dormancy. The underground plant part consists of the main taproot, of a variable number of secondary fibrous roots as well as of a rhizome, more or less expanded, containing buds, both single and gathered in groups. The one-year roots keep the absorption function until the spring, when they swell and gradually take on the reserve and support functions, while a new adventitious root system takes place adopting the absorption function. The cardoon’s root system is highly developed, being able to reach a depth of more than 1 m, which allows the plant to explore a significant volume of soil. In plants older than a year, the underground stem becomes increasingly evident; it is a rhizome, also commonly called *ceppaia*, which contains conducting cells and reserve parenchyma. Several buds differentiate on the rhizome surface, giving rise to side shoots called offshoots, which can grow up to form a new plant, thus expanding the rhizomatous fraction. In the epigeic part, cultivated cardoon has a ‘rosette’, since its stalk is very shortened (3–4 cm) and it has a high number of leaves (over 40), alternate and pinnate. Leaves can reach a length of more than 1 m (especially those basal); they are characterized by a well-developed petiole and a large midrib. The leaf lamina, crossed by numerous veins, could assume different shapes in different cultivars as well as within the same plant (heterophyllia). It is dark green coloured or ashen on the top page, greyish on the bottom page, because of its thick hairiness. At flowering, the plant has one or more erect flower stems, of variable height (1.5–3 m

approximately), each of which has a diameter of about 2–4 cm (Fig. 1.11). Stems are longitudinally ribbed, tomentose and very branched; they also have small leaves, alternate and lanceolate. Each branch has an inflorescence (head or capitulum) at its distal end, which has a round or oval shape depending on the cultivar. The plant has a large number of heads (10–30), the largest and earliest of which (main head) is on the top of the main stem; the heads of the next order (first, second, third and so on), progressively emitted, are gradually smaller. Each capitulum has several hundreds of flowers (florets), which are hermaphrodite, tubular and fitted in a well-developed receptacle (thalamus). At the full anthesis, the florets have very long stigmata (~5–8 cm). Florets are usually blue-violet coloured, although there are mutant genotypes having florets white or lilac coloured. Analogously to the globe artichoke, the fruit is an achene, endowed with a plummy structure—the pappus—which favours the dispersion by wind action (anemochorous dissemination). Thousand ‘seeds’ weight ranges between 20 and 40 g. From a biological standpoint, the cultivated cardoon is a perennial geophyte/hemicryptophyte herbaceous species, whose field duration is indefinite, thanks to the vitality of the rhizome. In the areas characterized by Mediterranean subarid climate, where the crop expresses its full production potential, the crop cycle is autumn–winter–spring, with a vegetative stasis phase in the summer, more or less prolonged, while in middle latitudes the vegetative stasis occurs between spring and autumn. In southern Italy, the cultivation cycle begins with the germination of achenes in the autumn, followed by a long vegetative phase, which lasts until the beginning of following spring. During this phase, the gradual transition to reproductive phase of the shoot apex occurs, and the first head starts to differentiate at late winter–early spring. The first head initially appears as a swelling in the centre of the leaf rosette and becomes more evident because of the main flower stem elongation. At the same time, other heads progressively differentiate on the top of the branches of main floral stem. The anthesis starts in the late spring (late May–early June)

and, of course, affects first the main head, then the other heads according to their order. At advanced flowering stage, each head has several hundred florets at a different development stage. In every single head, the flower development starts from the most peripheral florets and proceeds centripetally until the centre. In *C. cardunculus*, the flowering is dicogamous and, specifically, proterandrous. Indeed, the stigma becomes receptive from 4–5 to 8 days after anthesis, that is when the pollen, whose germination lasts 3–4 days, has already lost its vitality. Pollination is entomophilous, and reproduction is mainly by cross-fertilization, because of the previously mentioned proterandry mechanism. However, a small amount of self-fertilization between different inflorescences of the same individual (geitonogamy) is inevitable, due to their progressive ripening. Ripening of the achenes takes place starting from 50 to 60 days after anthesis and is accompanied by the progressive desiccation of the aboveground biomass. When achenes reach ripeness, they begin to be disseminated by wind (anemochorous dispersal), thanks to the disintegration of the receptacle and the peculiar structure of the pappus. Given the lack of dormancy mechanisms, except in some special cases (temperatures higher than 29–30 °C accompanied by anoxia), the ‘seed’ is readily germinable when favourable environmental conditions are met (sufficient soil moisture and temperatures between 14 and 24 °C). The vegetative regrowth after the summer is assured by the underground rhizome buds, which have remained dormant during the hot and dry season.

Archontoulis et al. (2010) described the cultivated cardoon phenological growth stages based on the Biologische Bundesanstalt, Bundessortenamt, Chemische Industrie (BBCH) scale. They defined nine principal growth stages as listed below:

- Principal growth stage 0: germination/sprouting/bud development
- Principal growth stage 1: leaf development
- Principal growth stage 2: formation of side shoots/tillering
- Principal growth stage 3: rosette growth



Fig. 1.11 Development in height of cultivated cardoon (photograph taken by Mauromicale)

gathered in groups. The stem is robust, simple and striated, it can be hairy or hairless, but without thorns. The basal leaves, arranged as a large rosette, are deeply engraved, pinnate, up to 35 cm long, white and hairy on the bottom surface, and with long spines at the edge (1–3 cm). Stem leaves are simple, alternate and spiny. The flowering axis is erect, branched, rugged, striated longitudinally and has alternate leaves. The main stem has branches with heads at their distal ends. The plant height is variable, from 40 cm up to 120–130 cm. The flowers (florets), hermaphrodite, tubular, characteristic of the Asteraceae, are grouped in an inflorescence (head or capitulum). Florets at full ripening can be 8 cm or longer, they are violet coloured, but there are mutant genotypes with white (Fig. 1.12) or pink florets. The fruits are tetragon-shaped or flattened achenes, dark greyish and mottled, combined with the calyx metamorphosed into a pappus, which promotes the anemochorous dissemination.

- Principal growth stage 4: development of vegetative plant parts
- Principal growth stage 5: inflorescence emergence and development
- Principal growth stage 6: flowering and capitulum formation
- Principal growth stage 7: development of capitulum and seeds
- Principal growth stage 8: capitulum and seed ripening
- Principal growth stage 9: senescence.

1.2.3 Wild Artichoke or Wild Cardoon

Wild cardoon is a typical geophyte species, perennial, capable of both sexual reproduction and agamic propagation. It has well-developed roots, with a taproot able to penetrate to a depth of about 1.5–2 m allowing the plant to tolerate water deficits, and a variable number of secondary roots. It has a rhizome, more or less expanded, containing buds, both single and



Fig. 1.12 Wild cardoon with white-coloured florets (photograph taken by Mauromicale)