Chapter 8
Globe Artichoke (*Cynara cardunculus* var. *scolymus* L.) Breeding

Fernando López-Anido and Eugenia Martin

Abstract Globe artichoke (*Cynara cardunculus* var. *scolymus* L.; Asteraceae) is a diploid (2n = 2× = 34), perennial, mostly cross-pollinated species native to the Mediterranean Basin. It represents an important component of the agricultural economy of southern Europe, and is grown for its large immature inflorescences, called capitula or heads. Artichokes have recognized nutraceutical properties for human health. Its commercial production is based mainly on perennial vegetatively-propagated clones. Recently its cultivation has been shifted toward seed-propagation of hybrids. Italy holds the richest biodiversity of cultivated *Cynara*, which has resulted in the culture of varieties and landraces adapted to specific local climatic conditions and markets. Cultivar-groups comprise early and late types, but also spiny, violet, Romanesco and Catanese types. Traditionally selections have been made within a given clone, removing off-types. Due to its heterozygous nature, a great variability is seen after crossing or selfings, promoting the selection of new cloned varieties. Seed-propagated hybrids are feasible upon the use of genic male sterility. In the past 20 years new technologies have been applied to broaden the knowledge of the molecular basis inherent, from the first genetic linkage map, the identifications of QTL for yield and related traits, up to the recent whole-genome sequence.

Keywords Capitula · Breeding · *Cynara* · Clones · Hybrids · Mediterranean

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8.1 Introduction

Cynara cardunculus L. is a diploid (2n = 2× = 34), perennial, mostly cross-pollinated species that belongs to the Asteraceae family, native to the Mediterranean Basin. The wild taxon [var. *sylvestris* (Lamk) Fiori] is recognized as the ancestor of globe artichoke [var. *scolymus* (L.) Fiori, ssp. *scolymus* (L.) Hegi] and the leafy cultivated cardoon (var. *altilis* DC) (Rottenberg and Zohary 1996). Globe artichoke represents an important component of the agricultural economy of southern Europe, and it is grown for its large immature inflorescences, called capitula or head (Bianco 1990). Fresh artichokes commonly are steamed or boiled, after which the fleshy bases of the outer bracts, the inner bracts, the receptacle and portion of the floral stem may be eaten (Fig. 8.1). Its commercial production is based mainly on perennial cultivation of vegetatively-propagated clones. However, in the last 20 years there has been a steady increase in the availability of new seed-propagated cultivars and hybrids, mostly from private seed companies. This has changed the situation, turning artichoke into an annual crop. Artichokes also have nonfood uses as their leaves are a source of antioxidant compounds, such as luteolin and dicaffeoylquinic acids (cynarin) (Di Venere et al. 2005; Gebhardt 1997) and the roots contain inulin, an oligosaccharide known to have a positive effect on human intestinal flora, thus on health (Raccuia and Melilli 2004). The cultivated cardoon is a minor seed-propagated crop, grown for its fleshy stems and leaf stalks, with some regional importance in Italy, Spain and southern France (Dellacecca 1990). For the past 20 years, the potential use of the species as an energy crop through its biomass production has been emphasized (Cravero et al. 2012; Foti et al. 1999; Gominho et al. 2018; Raccuia and Melilli 2010).

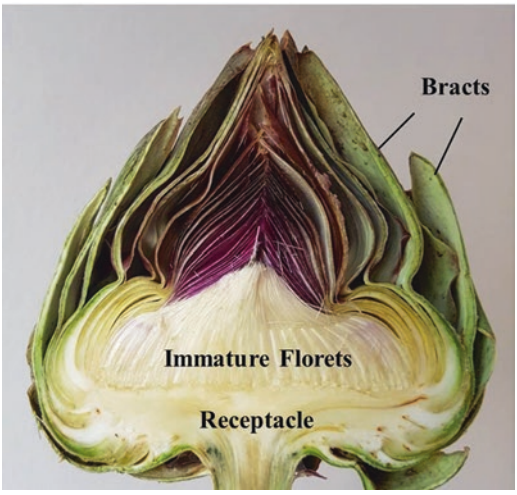

Fig. 8.1 Longitudinal section at the harvest stage of globe artichoke. (Source: Trizek 2018)

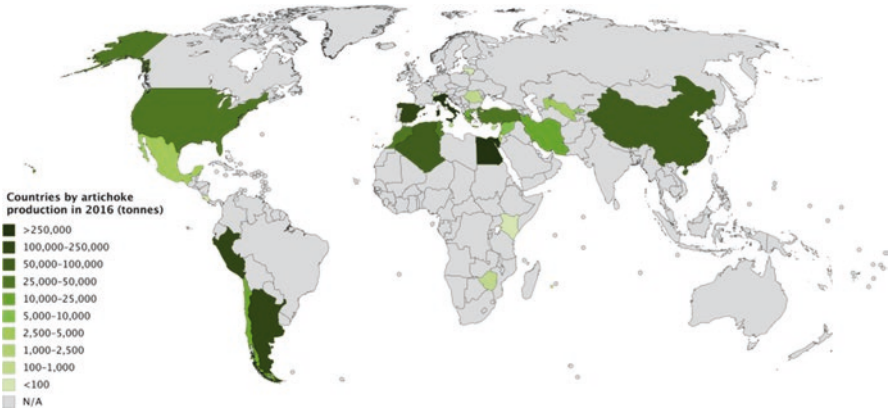

Fig. 8.2 Countries by globe artichoke production in 2016. (Source: JackintheBox 2018)

8.1.1 Economic Importance

Traditionally globe artichoke is cultivated in the Mediterranean countries, which account for almost 80% of the world's globe artichoke growing areas, where Italy and, in recent years, Egypt are major producers (Pesce and Mauromicale 2019). Other countries with a significant production outside the Mediterranean Basin are Peru, China and Argentina (Fig. 8.2). Spain is the most important exporter either as fresh or processed, accounting for about 60% of the traded market (Calabrese 2019).

8.1.2 Germplasm and Domestication

Eight species make up the genus *Cynara* by Wiklund (1992): *C. cardunculus* L., *C. syriaca* Boiss., *C. auranitica* Post, *C. cornigera* Lindley, *C. algarbiensis* Cosson, *C. baetica* (Spreng.) Pau, *C. Cyrenaica* Maire et Weiller and *C. humilis* L. This author placed *C. tournefortii* Boiss. et Reuter in another genus, but it was later included by Robba et al. (2005). More recently, natural spontaneous hybrid plants between *C. tournefortii* and *C. cardunculus* have been described in a sympatric wild population of both species (Blanca and Sánchez-Carrión 2014), supporting this inclusion. All wild species are perennial and the genus is characterized by large spiny leaves and heads. *Cynara algarbiensis*, *C. baetica*, *C. humilis* and *C. tournefortii* are principally of Western Mediterranean distribution, while *C. cornigera*, *C. Cyrenaica* and *C. syriaca* are distributed in the eastern part of the Mediterranean. *Cynara cardunculus* (hereafter wild cardoon), is present in almost all the Mediterranean, and reported to contain two wild subspecies, namely ssp. *cardunculus* and ssp. *flavescens* Wiklund; differing in their bract characters and geographical distribution: the former is distributed from Cyprus to Greece, Central and Southern

Italy, Sicily and Sardinia, and the latter is dispersed in Iberia and the Macaronesian Region (Wiklund 1992).

The domestication of these crops (globe artichoke and cultivated cardoon) is not yet fully understood, and when and where it occurred is still unknown. In a first hypothesis it was believed that both crops resulted from human selection pressure for either large, non-spiny heads (globe artichoke) or non-spiny, large stalked tender leaves (cultivated cardoon) in a single domestication event (Basnizki and Zohary 1994). Applying a molecular clock model, the divergence of cultivated cardoon dates to the beginning of the second millennium AD. Sonnante et al. (2002, 2004) using other molecular markers, such as random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP), indicated that wild cardoon germplasm appears genetically closer to leafy cardoon than to artichoke. The similarity of wild cardoon to cultivated leafy cardoon is also indicated by a number of nucleotide substitutions that are synapomorphic to these two taxa, especially in the ITS regions (Sonnante et al. 2007). In a parsimony consensus tree the wild cardoon accessions were placed closer to the domesticated cardoon than to the globe artichoke (Fig. 8.3). This is in agreement with the hypothesis that a second round of domestication took place in the northern/western range of the Mediterranean, leading to a seed-propagated crop, mostly utilized for its leaves (cultivated cardoon). The lower number of varieties present in cultivated cardoon (Dellacecca 1990) as compared to artichoke (Bianco 1990) is a further indication of a more recent domestication.

Hybridization experiments have demonstrated that wild cardoon and both cultivated species are genetically cohesive since they are completely interfertile and, therefore, they belong to the same gene pool (Basnizki and Zohary 1994; Rottenberg and Zohary 1996, 2005). Other wild *Cynara* species, in particular *C. algarbiensis* and *C. syriaca*, exhibit only limited capacity to set seeds and produce viable hybrids when crossed to the cultigen, while the remaining wild allies showed almost complete genetic isolation (Rottenberg and Zohary 1996).

8.2 Current Cultivation and Reproduction

8.2.1 Growth Habit and Inflorescence Development

The artichoke plant is a typical rosette, with leaf morphology varying in color and shape, depending on cultivar and position in the plant. Roots can penetrate up to 120 cm into the soil, and leaf number, thus size of the rosette, will be determined by the length of the vegetative stage. Floral induction requires a minimum accumulation of low temperatures coupled with long-day photoperiod (Basnizki 1985). The induction requirements will vary with the cultivar. During stem elongation, leaves become progressively narrower and shorter. The stem arises from the center of the rosette, whereas cultivation as perennial may produce several rosettes. The main

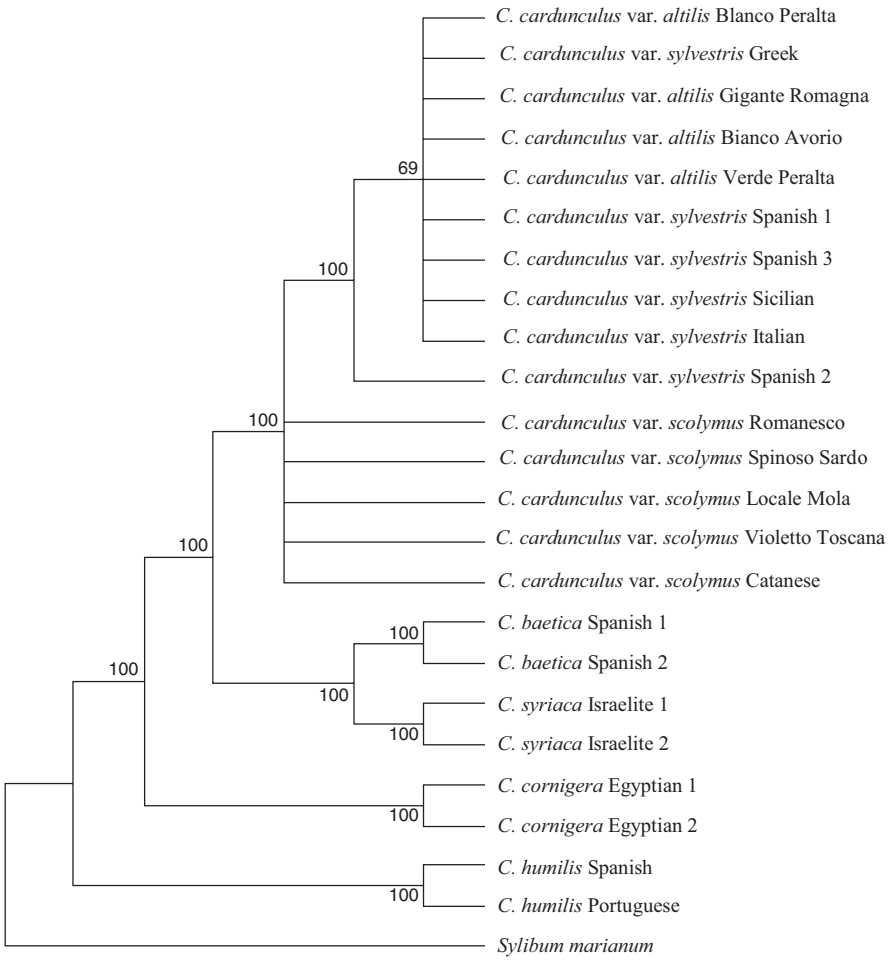

Fig. 8.3 ITS (internal transcribed spacers) parsimony consensus tree showing phylogenetic relationships among cultivated and wild *Cynara* accessions. (Source: Sonnante et al. 2007)

stem bears the main capitulum and ramifications terminated by capitula. The main or central capitulum is always the most voluminous, other capitula become smaller along the ramifications. Under dry summer of the Mediterranean environment, the aerial plant will desiccate after harvest is finished, and the underground stem will remain dormant until rain or irrigation is provided. Under temperate climate, growth from axillary non-induced buds will continue through the summer (Basnizki 1985).

8.2.2 Vegetative Propagation

Three methods of division are customarily practiced in vegetative propagation, which are related to different countries and climates. After the summer drought in the Mediterranean area, axillary dormant or semi-dormant buds borne on short swollen protuberances, with a limited root system, partially attached to the stump of the previous season plant, are separated and are referred as *ovoli*. The use of ovoli to establish new plantations of clonal varieties is widespread in Italy (Ryder et al. 1983). In Spain, it is preferred to divide the stump in pieces called *zuecas*, which contain dormant buds and attached roots. In temperate climates such as France and Argentina, axillary vegetative shoots that emerge from the base of the stump, with some root development, are called *suckers* or *hijuelos*, which are detached and used as propagules.

8.2.3 Floral Biology

The floral biology of globe artichoke has been studied in detail by Foury (1967). It is a predominately a cross-pollinated plant. Cross-fertilization is promoted by protandry. Selfing can be simply accomplished. On most cultivars a first order capitulum contains 800–1400 florets. Anthesis begins with the peripheral florets and along the subsequent 2–3 days progresses centripetally. In each floret the anthers mature first and the unreceptive style pushes the pollen upward. At this time, if crosses or selfings are pursued, pollen collections should be conducted daily between midmornings until noon, in previously bagged capitula. The two stigmatic surfaces of the florets mature 2–3 days after the last central florets finish shedding pollen. At this point, previously collected pollen should be applied using a paint brush in order to obtain selfed or crossed seeds, always maintaining the receptive capitula bagged so as to avoid pollen contamination. Pollen brushing can be repeated for 2 days in order to assure seed set. Pollen remains viable at 2–4 °C for up to 10 days (Foury 1967).

8.2.4 Seed Cultivation

Research aimed at the possibility of obtaining seed-planted materials of globe artichoke has been conducted over the past 50 years (Foury 1979; Pécaut et al. 1981; Porchard et al. 1969). The shift towards seed reproduction was highlighted in order to prevent the spread of soil-borne pathogens and viruses, commonly propagated with the stem pieces and buds; improve soil exploration by long vertical taproots secured by seed-derived plants; convert the crop into an annual and facilitate rotations and develop seed and nursery industry. Due to the high heterozygosity of the

clonal varieties, a great array of segregation appears after selfings, which hinders the attainment of seed-propagated varieties with similar head characteristics and precocity, to the well-adapted vegetatively-cloned varieties (Basnizki and Zohary 1994). Also inbreeding depression for plant vigor and pollen production counteracts the advancement of inbred lines beyond three or four generations of selfings (Foury 1979). However, in crosses, the recovery of hybrid vigor for yield attributes (Pécaut and Foury 1992), and the detection of genic male sterility (Basnizki and Zohary 1998; Principe 1984) has encouraged, in recent years, seed companies to create hybrid cultivars (Big Heart Seed Co 2019; Nunhems 2019).

8.3 Cultivated Gene Pool

Italy holds the richest biodiversity of cultivated *Cynara*, which has resulted in the local culture of many types of varieties and landraces, very often well adapted to specific local climatic conditions and markets (Dellacecca et al. 1976; Elia and Miccolis 1996; Pagnotta and Noorani 2014). This stability of phenotypes make clonal systems attractive for domestication, as any novelty could be fixed by the asexual reproduction. In grapes (*Vitis vinifera*), a species also with a great array of adapted clones, it has been demonstrated that along the domestication history, new variants accrued mostly hemizygously and are locked-in by clonal propagation (Allaby 2019).

8.3.1 Cultivar Groups

Many studies have been conducted to classify the great number of artichoke landraces or clones available (Dellacecca et al. 1976; Elia and Miccolis 1996; Lanteri et al. 2004; Pagnotta et al. 2017). A first criterion is the harvesting time or cycle, which divides the cultivars into early or late types. The early types are harvested in autumn and spring, and are considered remontant or re-blooming, that means that they have two flowering periods, one in autumn and the second in spring. Typical of this group are Violet de Provence, Catenese, Violet d'Algerie, Tudela, Spinoso Sardo and Sakiz. The late types produce only in spring, Romanesco, Green Globe, Camus de Bretagne, Violetto di Toscana, among others, belong to this group (Dellacecca et al. 1976; Lanteri et al. 2004).

The second criterion classifies cultivars on the basis of the morphology of the capitula. In particular, the characteristics taken into consideration are: shape, color and the presence of spines (Fig. 8.4). It is therefore possible to identify four groups: Spiny with long sharp spines on both bracts and leaves, Violet with violet-colored capitula, Romanesco with spherical or sub-spherical non-spiny capitula and Catanese with relatively small, elongated non-spiny capitula. The Spiny and Catanese types are normally of the re-blooming typology, while Violet and

Fig. 8.4 Different morphology of capitula. (**a**) Spherical green, (**b**) Spherical plain violet, (**c**) Spiny elongated, (**d**) Sub-spherical variegated. (Photos **a**, **b** and **d** by F. López-Anido; Photo **c** Source: Radiuk 2013)

Romanesco varieties are usually harvested in spring (Pagnotta et al. 2017). Figure 8.5 presents the results from a cluster analysis conducted in order to classify accessions by phylogenetic groups based on diversity (Lanteri et al. 2004).

8.3.2 Variation in Early Mediterranean Cultivars

Natural occurring variation in some early cultivars was first reported by Porchard et al. (1969). It was considered chimeric, which produces the so-called Bull and Pastel variants. In cv. Violet de Provence, of normal elongated capitula, plants derived from the first mutation, have almost spherical heads and less pinnatifid leaves. On the contrary, Pastel plants possess noticeable pinnatifid leaves and are late bolting (spring). These variations were later described as emerging after in vitro multiplication of early cultivars, where the Bull type resulted from the tetraploid nature. The sexual progeny failed to maintain entire leaves, and resulted in all of the Pastel type (Pecaut and Martin 1993). Recently, Cerruti et al. (2019) identified different methylation patterns between true-to-type and off-type leaves of plants from Spinoso Sardo, another early Mediterranean cultivar, and suggested an epigenetic control related to differences in precocity and vegetative development. It is

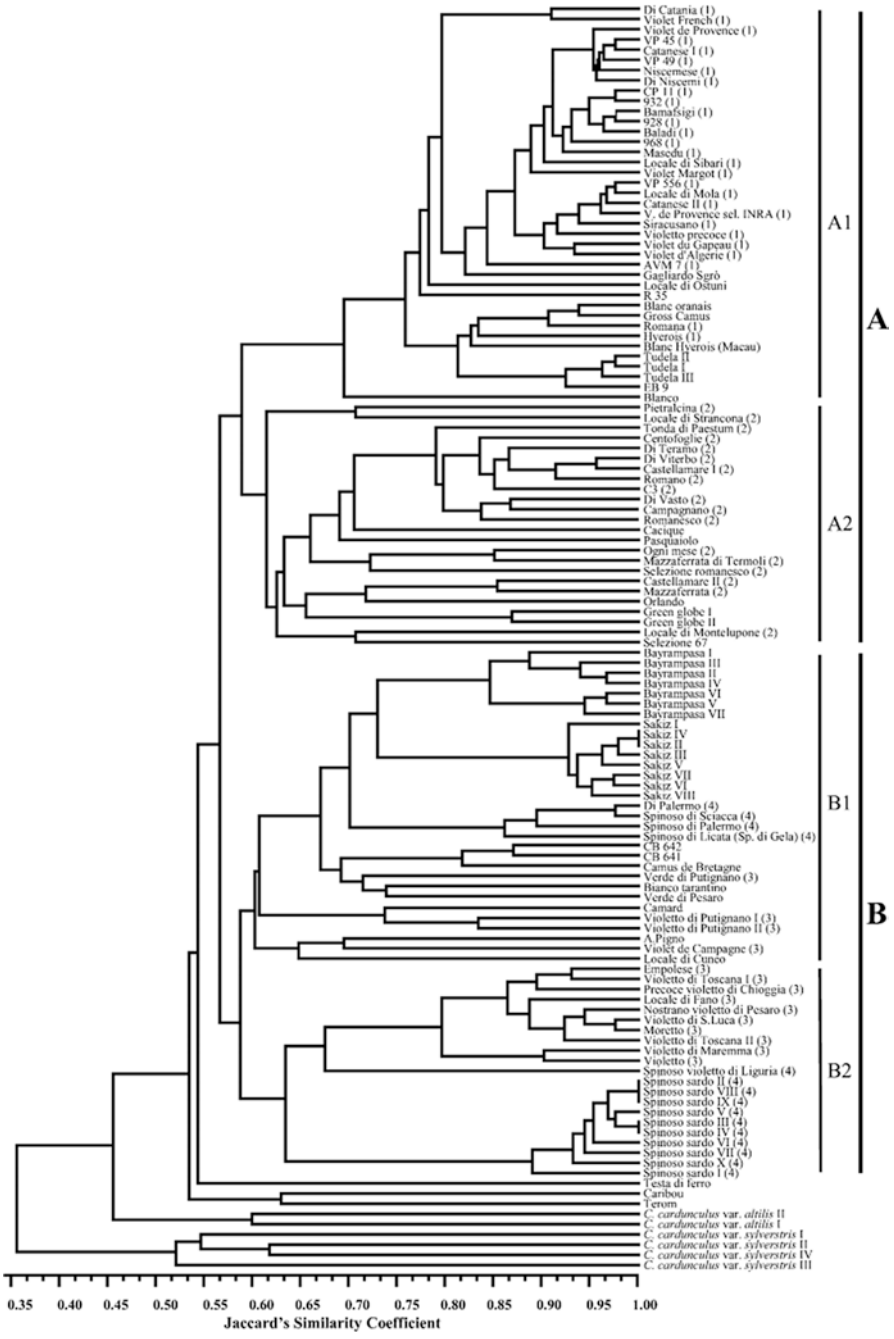

Fig. 8.5 Dendrogram obtained from UPGMA cluster analysis of AFLP data. Subcluster (**a1**) Catanesi type, (**a2**) Romanesco type, (**b1**) Violet type and (**b2**) Spiny. (Source: Lanteri et al. (2004))

interesting from the domestication point of view how this early variant emerged in different areas and as types of cultivated capitula (green, violet, spiny). In grapes, concurrent selections have also been evidence of a domestication syndrome trait (Zhou et al. 2019).

8.4 Germplasm Conservation

8.4.1 Living Collections

The characterization and conservation of *Cynara cardunculus* germplasm is now of international concern. Addressing this, the European Commission (Directorate-General for Agriculture and Rural Development under Council Regulation (EC) No 870/2004) sponsored the European Project CYNARES (Pagnotta and Noorani 2014). The project (2008–2012) has seven partners from France, Spain and Italy (Table 8.1), who share European germplasm collections which have been assessed at the morphological, biochemical and molecular levels, as well as for disease resistance. Conservation of *C. cardunculus* germplasm has been undertaken based on the

Table 8.1 Main collections and accessions held of *Cynara*

Collection centers	Living accessions held
Collection at University of Tuscia and ENE, Italy http://www.unitus.it/ http://www.old.enea.it/com/ingl/default.htm	Artichoke: Romanesco, Montelupone A, Montelupone B, Jesino, Ascolano, Bianco di Pertosa, Tondo Rosso di Paestum, wild and cultivated cardoon
Collection at Cartagena University, Spain https://www.upct.es/	Artichoke: INIA-D, INIA-B, ITGA, Clon 303 and Cabeza de Gato, Spinoso Sardo, Moretto, Salambo, Violet de Provence and Macau; cultivated cardoon: Blanco de Valencia, Blanco de Huerva, Sarramian, Verde Calahorra, Blanco Peralta, Del Cortijo, Verde de Huerva, Lleno de España, Rojo de Agreda and Verde Peralta
Collection at ITGA, Spain https://dialnet.unirioja.es/	Artichoke: ITGA selection, Cabeza Gato, INIA D, PAT-89, Carderas, Camus de Bretagne, Salanquet, Crysantheme, Camerys, Macau, France, Calico Rojo, Calico Verde, C-3, VP-41, Hydes, Apolo, Brindisi, Campagnano, Hysponos, Italiana, Masedu, Moretto and Mutación Romanesco, Criolla; cultivated cardoon: Acequi, Blanco de la Huerva, Blanco de la tierra, Blanco de Peralta, Blanco de Valencia, Blanco Francés de Valencia, C-001-Rosa de Agreda, C-002-Blanco, C-003-Cadrete, Cimbro, Del Cortijo-Arsenio
Collection at Groupe d'Etudes et de Contrôle des Variétés et des Semences (GEVES), France https://www.geves.fr/catalogue-france/	Artichoke: Gros Vert de Laon, Petre, Vert de Provence, Chrysanteme, Camus de Bretagne, Blanc Hyerois, Violet de Provence, Cardinal, Calico, Popvert, Salambo

Convention on Biological Diversity, the FAO Global Plan of Action for Plant Genetic Resources for Food and Agriculture and the International Treaty on Plant Genetic Resources for Food and Agriculture. France, Italy and Spain were key project partners as traditional artichoke cultivars are grown predominantly in these Mediterranean countries.

8.4.2 In Vitro Conservation

Conservation of globe artichoke by tissue culture offers an alternative method to produce large, homogeneous and disease-free populations, and enabling in vitro storage of selected genotypes (Bekheet and Sota 2019). Ancora et al. (1981) and Morone-Fortunato et al. (2005) developed in vitro techniques for micropropagation and short-term conservation of cv. Romanesco. Bedini et al. (2012) optimized in vitro cultures of four Tuscan globe artichoke cultivars: Terom, Violetto di Toscana, Chiusure and Empolese. Moreover, in vitro medium-term storage of globe artichoke cv. Balady was recognized (Bekheet 2007). Shoot bud cultures were stored under aseptic conditions at 5 °C or osmotic stress. The results indicated that storage at the low temperature was obviously effective compared with storage on medium containing osmotic stress agents. For long-term storage, cryopreservation, i.e. storage at ultra-low temperature, usually in liquid nitrogen (−196 °C), is the current method. At this temperature, all cellular divisions and metabolic processes are stopped (Engelmann 2010).

8.5 Traditional Breeding

Compared to other vegetables, globe artichoke breeding has a limited recorded history. The different approaches followed so far are enumerated below.

8.5.1 Intraclonal Selection

Most clonal varieties are landraces maintained over time by vegetative means, where any spontaneous somatic mutations in buds can be passed to the next clonal progeny. As discussed above, in the early Mediterranean cultivars, the occurrence of such variations was frequent, thus many breeding efforts have been aimed at purging clonal varieties of these off-type plants (Abbate and Noto 1981; Deidda 1967; Pécaut 1983). However, the progress that can be accomplished is limited by the average performance of the clone variety itself.

8.5.2 Interclonal Hybridization

Due to the high heterozygosity nature of the clonal varieties, after selfing or hybridization, a tremendous array of variation appears. In the progeny, any plant combining desirable attributes can be cloned, and given enough time constitute a new clonal cultivar. In this context efforts have been aimed at improving earliness, capitula yield and quality (Foury 1969; López-Anido et al. 2005; Miller 1975; Scarascia-Mugnozza and Pacucci 1976; Tesi 1976). Most of the productive characters are of quantitative gene inheritance, thus in a segregant population relatively good progress could be attained. López-Anido et al. (1998) estimated that in a reference population composed of different cloned varieties, and selection intensity of the best 5% clones, the expected selection gain could be greater than 30% of the population mean for weight of secondary capitula, weight of the bottom of the first capitulum, harvest period and total capitula yield.

8.5.3 Breeding Seed Grown Varieties

As already mentioned, in recent years great efforts have been made to implement a seed-cultivation system. The first seed varieties were the result of inbreeding and selection, attempting to create a true-breeding form comparable, in vigor and yield, to the parent stock (Basnizki and Zohary 1994). Talpiot (Basnizki and Zohary 1987) and Imperial Star (Schrader and Mayberry 1992) were the first seed-planted cultivars available, both released through public breeding programs. Later hybrid seed-planted varieties appeared as the result of programs by private seed companies (Big Heart Seed Co 2019; Nunhems 2019). Regarding the component of variation that is involved when dealing with selection and hybridization, for the majority of the productive characters, the general combining ability variance (additive effects) turned out to be of greatest importance. The specific combining ability variance (non-additive effects) was only significant in the case of the weight of the main capitulum and receptacle (Cravero et al. 2004). Another approach relative to seed-planted cultivars is the search for an open-pollinated variety by means of recurrent selection of a given population. This seems plausible in the case where the original population has already been fixed for quality characters like spinelessness or color characteristics (green, violet), and further selection could be applied to capitula shape, cycle or yield itself (Martin et al. 2010).

8.6 Molecular Breeding

8.6.1 Molecular Markers

Molecular studies applied to understand the genome and genomic sequence of globe artichoke started about 20 years ago. Initial studies focused on evaluation of the genetic variability in germplasm collections composed of several globe artichoke varieties and landraces. Usually, these studies included the evaluation of accessions of cultivated cardoon and wild cardoon, since they are considered botanical varieties of the same species. Several molecular markers such as RAPD (Lanteri et al. 2001; Sonnante et al. 2002), AFLP (Acquadro et al. 2009; Lanteri et al. 2004; Pagnotta et al. 2004; Portis et al. 2005), microsatellite (Acquadro et al. 2003, 2005; Sonnante et al. 2008), sequence-related amplified polymorphism (SRAP) (Casadevall et al. 2011; Cravero et al. 2007, 2019) and indels (Scaglione et al. 2009) were applied in genetic diversity studies. In general, these studies showed significant genetic distances among and within cultivars as the result of the multiclonal origin of most landraces, as discussed previously. Moreover, certain research results revealed that some varieties, called by different names at different locations, are duplications with the same molecular characterization.

Breeding approaches using molecular techniques were applied by Martin et al. (2008) to identify molecular markers linked to important traits such as capitula color and earliness. Applying SRAP markers in a F_2 segregating population and a BSA (bulk segregant analysis) strategy, they reported two molecular markers associated with both traits. The marker Me4-Em4 (~850 bp) was associated with green head color, whereas Me3-Em5 (~520 bp) was linked to late production. The same type of molecular marker in combination with simple sequence repeat (SSR) were applied by Reolon da Costa et al. (2016a) to evaluate the homozygosity advance rate after two cycles of recurrent selection in Brazilian artichoke germplasm.

8.6.2 Genetic Linkage Maps

To understand the genome and genomic position of important agronomic traits in *Cynara cardunculus*, based on molecular marker technologies, a number of studies have been carried out to develop genetic linkage maps of the species. Up to now, five linkage maps of the species have been developed as a scaffold of localized important agronomic traits and to understand the genome of the species. Segregating populations were obtained by initial crosses between diverse genotypes of the three botanical varieties of the species (globe artichoke, cultivated cardoon, wild cardoon) following a double pseudo testcross mapping strategy, which is considered the most efficient way to construct genetic linkage maps in outcrossing species. The first linkage map was reported by Lanteri et al. (2006), using AFLP, microsatellite-amplified fragment length polymorphism (M-AFLP) and sequence-specific

amplification polymorphism (S-SAP) markers to genotype 94 individuals of a F_1 population generated from a cross between two globe artichoke clones (Romanesco C3 x Spinoso di Palermo). A total of 204 loci were mapped in the female map with a covered 1330.5 cM, whereas the male map comprised 1239.4 cM with 180 loci mapped. The same maps were enhanced by Acquadro et al. (2009) using a set of microsatellites developed for the species. Moreover, genes related to the caffeolquinic acid pathway and associated single nucleotide polymorphisms (SNP) markers were included in the linkage maps (Comino et al. 2007, 2009; Menin et al. 2010, 2012; Moglia et al. 2009). A second segregating population obtained by crossing Romanesco C3 artichoke clone with the cultivated cardoon Altilis 41 was developed by Portis et al. (2009) and linkage maps presented for both progenitors. The Romanesco C3 map included 326 loci with an overall length of 1486.8 cM, whereas the Altilis 41 map was 1015.5 cM and included 176 loci. Based on the two maps available for the globe artichoke clone Romanesco C3, a reference linkage map of the species was developed (Portis et al. 2012) including 172 microsatellite-derived expressed sequences (Scaglione et al. 2009). Following the same mapping strategy, other segregating populations were generated. Sonnante et al. (2011) developed a linkage map from an initial cross between the globe artichoke Mola and the wild cardoon Tolfa, both genotypes from the Mediterranean Region. The set of 192 F_1 individuals was genotyped by SSR, AFLP and SNP markers related to genes involved in the chlorogenic acid synthesis. The integrated map included 337 loci and covered 1488.8 cM. Using Argentinean genotypes of wild cardoon and Estrella del Sur artichoke, Martin et al. (2013) developed new linkage maps of the species (Fig. 8.6). The main backbone of the maps was SRAP markers and other type of markers were included such as SSR, AFLP and SNP linked to genes involved in the caffeolquinic acid pathway, in order to compare these maps with the reference maps reported by Portis et al. (2012). The female linkage map (wild cardoon) was 1465.6 cM and included a total of 214 loci, whereas the male map was 910.1 cM and comprised 141 loci. A comparison between both mapped parents showed that the wild cardoon map was some 50% longer that the globe artichoke one, reflecting that the heterozygous level in the wild cardoon was higher than in the domesticated form. On the other hand, Estrella del Sur is an open-pollinated commercial variety stabilized for some key agronomic traits, and this selection process would have reduced its heterozygosity.

8.6.3 Identification of Genome Regions Linked to Important Traits

8.6.3.1 Single Locus and Quantitative Trait Loci

Most linkage maps of the species were used to identify and localize regions of certain agronomic important traits, from single locus to quantitative trait loci (QTLs). Loci encodings of single traits such as presence of spines in capitula, leaves and

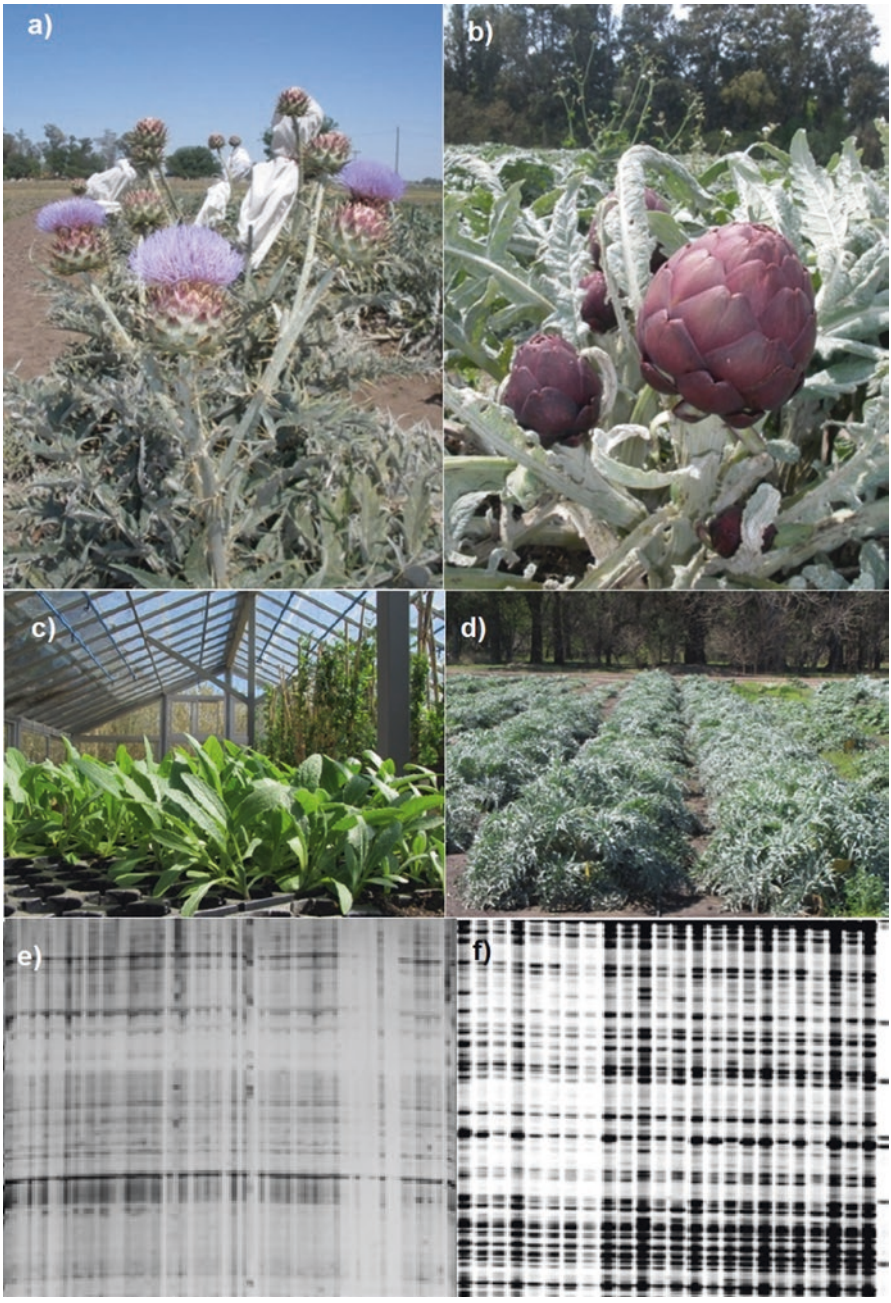

Fig. 8.6 (**a**) Argentinean genotypes of wild cardoon, (**b**) Estrella del Sur globe artichoke used as a progenitor to develop new genetic maps of the species (Martin et al. 2013), (**c**) F_1 mapping population at nursery, (**d**) Same F_1 at field of the Experimental Station of Agronomy College of the Rosario National University, (**e**) Molecular analysis of the segregating SRAP loci, (**f**) AFLP loci. Photos by Eugenia Martin

head color were identified and mapped. Lanteri et al. (2004) reported a segregation ratio of 1:1 for the spines on leaves and bracts of capitula, which was reported to be controlled by a single locus with two alternative alleles: non-spiny (*Sp*) dominant to spiny wild allele (*sp*) (Basnizki and Zohary 1994). The locus was localized on the LG 16 of the maternal map, flanked by the two SSR (CMAFLP-08, CMAFLP-07). The presence/absence of spines on capitula was evaluated by Sonnante et al. (2011) and they observed the same 1:1 segregation ratio. The spiny locus was localized only in the maternal map and at 26.5 cM from the molecular marker CyEM-188. Martin et al. (2013) evaluated the spines in leaves and capitula separately. They observed that each trait is controlled by a single locus with two alternative alleles, one for spines in leaves (SpLeaf) and the other for spines on the capitula (SpHead). The two loci were localized at the LG 8 of the male map, at a distance of 6.5 CM between them, and at 9.0 cM from the SRAP marker Me4-Em3.685. The same authors evaluated head colors and observed a segregation consistent with a monogenic 1:1 ratio for purple-green versus purple capitula. The locus responsible for head color (ColorHead) was located at LG 5 of the female parent, at 17.5 cM from the SRAP marker Me4Em3.350. These results are in agreement with Cravero et al. (2005), who found a recessive allele (*p*) acting epistatically over a second locus *U*. In homozygosis *pp* determines green head whatever allele is present in the *u* locus. Otherwise, the capitula are variegated (Fig. 8.4) when a dominant allele *U* is present or plain violet, when recessive homozygosis (*uu*). The locus mapped by Martin et al. (2013) is the *U* locus of Cravero et al. (2005). Earliness was evaluated by Portis et al. (2012), in the F_1 progeny from Romanesco C3 x Altilis 41. Both parents and F_1 progeny were assessed over two seasons, 19 QTLs were identified and mapped in 7 regions of the consensus map; however, no individual earlier than the globe artichoke parent was found.

Another key important trait is yield and its components. QTLs associated with yield were reported by Portis et al. (2014) and Martin et al. (2016a) in different background crosses. Strong positive correlations between diameter, length and fresh weight of the main capitulum and second order heads were observed. These results suggest that indirect selection might be applied for heavier first order capitulum. Moreover, some transgressive individuals were observed in both mapped populations for most of the evaluated traits. Several QTLs per trait were identified and QTL for correlated traits were frequently co-localized, presumably due to pleiotropy. Since some QTLs identified by Martin et al. (2016a) (Fig. 8.7) were co-localized in the same mapping regions and coincided with those reported by Portis et al. (2012), these regions should be further targeted in order to assist breeding programs aimed at yield increase.

8.6.3.2 Male Sterility Loci

As already discussed, in recent years the artichoke seed market has been trending toward seed-propagated hybrids. In this context, since hand-emasculation is impractical, it is necessary to have an efficient method to produce hybrid seeds by male

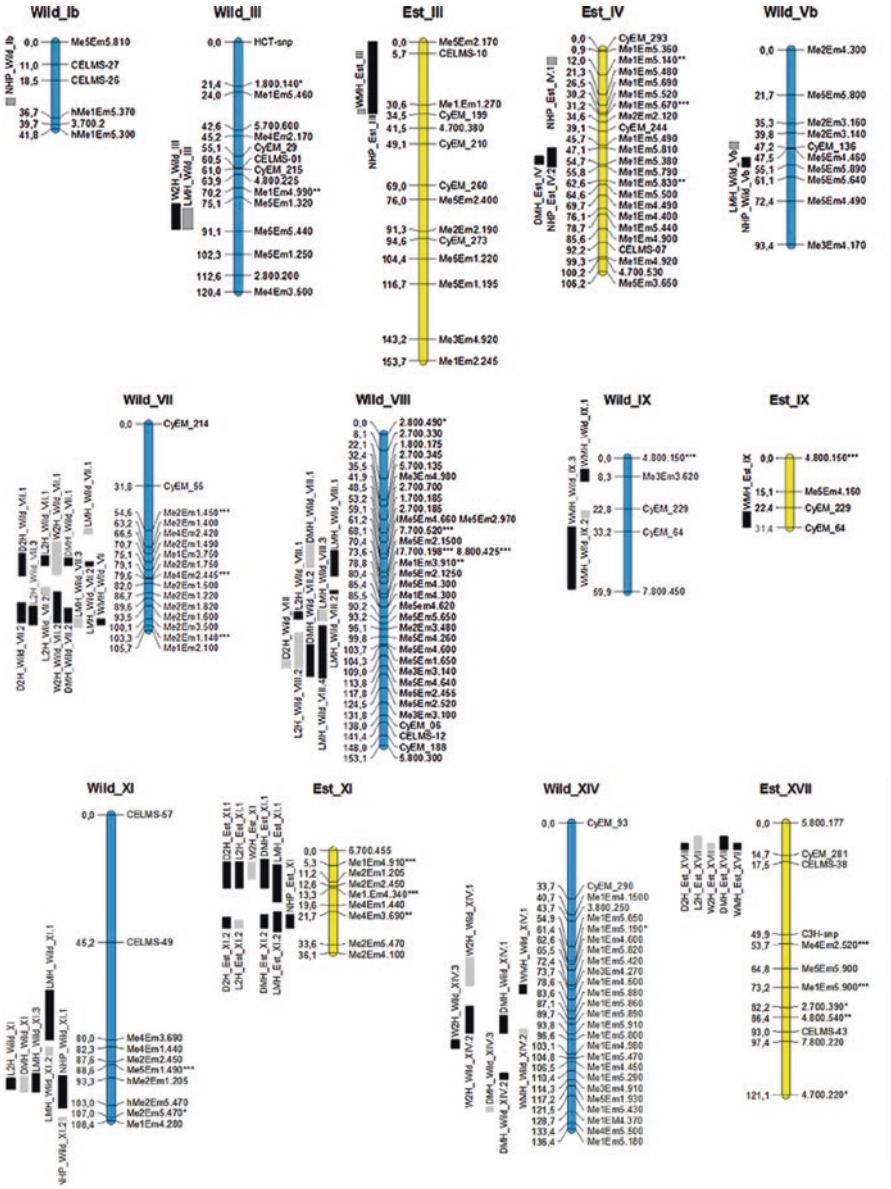

Fig. 8.7 QTLs for yield-related traits identified and mapped by Martin et al. (2016a, used with permission). Number of head per plant (NHP), fresh weight, diameter and length of the main head (WMH, DMH, LMH) and fresh weight, diameter and length of the second heads (W2H, D2H, L2H). Wild cardoon LGs in blue, globe artichoke Estrella del Sur LGs in yellow. Markers showing significant levels of segregation distortion are indicated by asterisks. Each QTL is represented by a bar, black bars show QTL detected in both seasons, while grey bars show QTL only expressed in the first season

sterility (MS). Although nuclear male sterility was reported in the species, the genetic base of this phenomenon is not clear. Principe (1984), in a half-sib family of a selected parent of unknown origin proposed a single recessive model of inheritance, where the male-sterile plants are in a homozygous recessive stage (ms1ms1). Two additional genes related to male sterility were reported by Basnizki and Zohary (1994) and designated ms2 and ms3. The first one was found in a progeny of Cavo origin and produced aborted pollen grains with an irregular form, similar to that observed for ms1, whereas ms3 was from a Tudela progeny, producing totally sterile anthers (Basnizki and Zohary 1998). Stamigna et al. (2004) and López-Anido et al. (2016) found in F_2 populations from French MS and Italian fertile clones a digenic inheritance, fitting a 15 fertile: 1 male sterile segregating plants. In this context, Zayas et al. (2020) extended the analysis incorporating SRAP markers and the BSA approach to identify associations with the ms loci. The evaluation included field screening of all the plants for pollen production over two seasons, quantification of pollen grain by microscopy and viability testing by using lactophenol-aniline blue stain (Fig. 8.8). Applying SRAP markers, they detected three associated with male-sterility (SRAP 7-10.1174, SRAP 4-9.700, SRAP 4-9.332) at a distance of 0.5 cM, 13.9 cM and 4.3 cM, respectively, from the ms locus. The markers were generated by the non-specific primer combinations Me7-Em10 (SRAP 7-10.1174) and Me4-Em9 (SRAP 4-9.332 and SRAP 4-9.700), with a size of 1774 pb for SRAP 7-10.1174, 700 bp for SRAP 7-10.1174 and 332 bp for SRAP 4-9.332.

8.6.3.3 Nutritional Quality

The genus *Cynara* has been proposed as a source of biocompounds with pharmaceutical and nutraceutical properties due to its polyphenolic contents (Ceccarelli et al. 2010; Reolon da Costa et al. 2016b; Rotondo et al. 2020). The polyphenolic content in leaves and capitula were reported for several commercial varieties and segregating populations (García et al. 2016; Moglia et al. 2008; Pandino et al. 2011, 2012). Although the polyphenols content is strongly influenced by the growing environment and the plant developmental stage, some genetic determination can be identified and used to improve new cultivars with higher levels of these compounds. Pandino et al. (2015) observed transgressive segregation for dicaffeolquinic acid in leaves of a F_1 population from a cross between globe artichoke and cultivated cardoon of the Mediterranean Region. The transgressive individuals were selected and evaluated over two growing seasons for its polyphenol profile, including dicaffeolquinic acid, apigenin, luteolin and narirturin, and were genotyped with microsatellite markers. From the selected individuals, two plants were identified that accumulate dicaffeolquinic acid and, if properly cloned, these genotypes could be used to source pharmaceutical compounds. A first approach to elucidated QTL association to the content of some polyphenols, chlorogenic acid and cynarin, in capitula, was reported by Martin et al. (2018), in a segregating population obtained by crossing Argentinean genotypes of wild cardoon x Estrella del Sur. Through a regression model, 11 SRAP markers associated with chlorogenic acid, and 11 SRAP

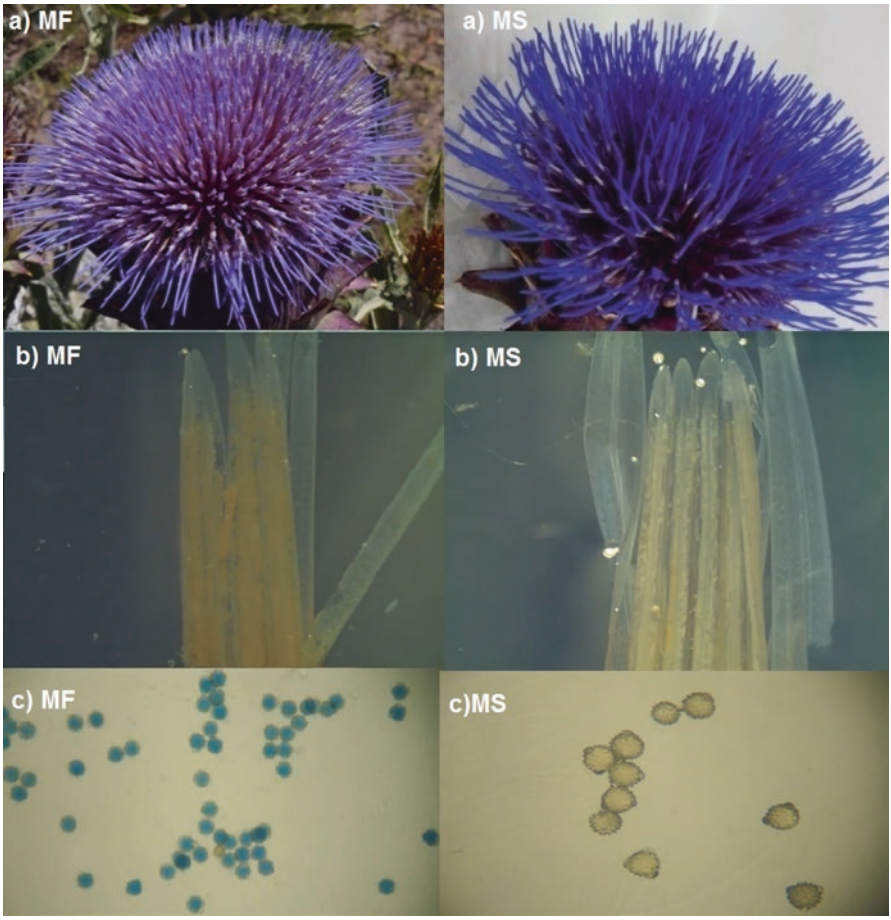

Fig. 8.8 Evaluation of male sterility in *Cynara cardunculus*. (**a**) Male fertile (left) and male sterile (right) capitula at anthesis, (**b**) Anthers of male fertile (right) and male sterile plants (left), (**c**) Pollen viability test by lactophenol-aniline blue stain, MF (male fertile plant), MS (male sterile plant). Photos by Aldana Zayas and Marta Bianchi

linked to the cynarin content, were identified. The proportion of the phenotypic variance explained by each QTL-marker was 12.8–34.4% for chlorogenic acid and 13.1–32.7% for cynarin content. In recent years, this approach to identify genomic regions linked to polyphenols content has expanded to include some flavonoids (apigenin, luteolin) and the evaluation of the genotypes under different environments conditions.

8.6.3.4 Biomass Production

As previously mentioned, cultivated cardoons are the most suitable taxa to be considered as an energy crop, as well as the remnant biomass of globe artichoke after harvesting the capitula. In this context, some efforts have been made to identify and localized QTLs related to biomass productions. Martin et al. (2016b), using the same mapping population previously described, studied five morphological traits associated with biomass production: diameter and height of the plant, dry weight of the leaves, capitula and stalks. The correlation among traits showed that the diameter of the plant has a strong positive association with height of the plant (0.70) and dry weight of the leaves (0.66); whereas dry weight of the capitula showed a highly positive correlation with dry weight of the stalks (0.92). Transgressive individuals were identified, mostly for diameter and plant height. Applying standard interval mapping, except for dry weight of stalks, 16 QTLs were observed for all remaining evaluated traits. Moreover, correlated traits were frequently co-localized at the same genomic region (Martin et al. 2016b). A second study was reported by Portis et al. (2018). They evaluated 11 traits related to biomass over two growing season, in a mapping population originated by the cross of a globe artichoke genotype and a cultivated cardoon from the Mediterranean Region. Correlations between traits were in accord with those of Martin et al. (2016b); applying a multiple QTL mapping strategy, a total of 27 genomic regions for biomass production were identified. The localization of some QTL in the linkage maps was consistent with reports by Martin et al. (2016b), in particular at LG 3 and LG9.

8.7 Genome Sequencing

Recent advances in new DNA sequencing technologies have simplified the acquisition of information about the genomes of more than 100 plant species, and numerous plant genomes are in the process of sequencing and assembly. Construction of a reference genome in an outbreeding species, with high heterozygous levels as globe artichoke, is laborious. Nevertheless, a reference genome of globe artichoke was developed using a clone obtained by three cycles of selfing, with a residual heterozygosity level of about 10% (Scaglione et al. 2016). The reference genome was generated by assembly 133.7 Gb sequencing data into ~13,000 scaffolds obtained using a Illumina HiSeq2000 platform, covering 725 Mb of the genome (67%). The re-sequencing of the genome parents of the mapping population (Portis et al. 2009) and genotyping by sequencing of the F_1 individuals allowed anchoring the scaffolds onto the 17 chromosomes of the species. The reference genome and all data information are available in the public domain database (http://www.artichokegenome.unito.it/cymsatdb/) (Portis et al. 2016). The information on the genome sequences provides the possibility of new genetic assays, assessment of the genetic diversity, gene isolation and marker-assisted breeding.

8.8 Genetic Engineering

Most of the production and consumption area of the artichoke is within the boundary of the European Union, because of this, research aimed at the use of genetic engineering to improve a given clone or cultivar has been discouraged. Also an overlap of distribution exists between the crop and the compatible wild cardoon, not only in the Mediterranean Region, but also in the USA, Argentina and Chile, which could facilitate gene escape, thus hindering any attempt to approve genetic engineering of cultivars.

8.9 Conclusions and Prospects

Globe artichoke is a vegetable crop with a limited breeding history; most attempts in the past were aimed at the purging of given heirloom-cloned varieties already adapted and accepted in local markets. Research on floral biology and advances in sexual reproduction turned the crop into a seed-propagated plant, suitable for annual rotations, which in turn can prevent the spread of soil-borne pathogens and viruses. Sexual reproduction facilitated the study of the inheritance of important traits (head color, presence of spines, male sterility), developed seed and nursery industries, and over the past 20 years a great array of molecular markers became available and positioned in linkage maps. Recently a reference sequenced genome was developed. Nevertheless, in contrast to other vegetables, the number of newly-released cultivars is limited, and a great proportion of the planted area is still covered with traditional cloned varieties. One of the possible reasons for this situation is the failure to obtain, by the classical breeding methods, seed-propagated materials of the early Mediterranean types, with autumn and spring production. The prospect for the next few years should be to attain these types of cultivars. Aiding in the pursuit of this goal may be the clustered regularly interspaced palindromic repeats (CRISPR)/CRISPR-associated 9 (Cas9)-mediated genome editing technology, which has been proven effective in many horticultural crops (Xu et al. 2019), coupled with genomic selection, in order to eliminate exogenous DNA of the editing tools (Voss-Fels et al. 2019).

Appendices

Appendix I: Research Institutes Relevant to Globe Artichoke

Institute/Organization	Specialization research activities	Contact information and website
Università degli Studi della Tuscia, Tuscia University	Genetic diversity, management	Prof. Mario-A. Pagnotta Va S.Maria in Gradi 4 01100 Viterbo, Italy pagnotta@unitus.it
National Agency for the New Technologies, Energy and the Environment (ENEA)	Genetics resources, genetics, in vitro culture	Paola Crinò Lungotevere Grande Ammiraglio Thaon de Revel 76 00196 Rome, Italy
Institute of Science of Food Production – Institute of Biosciences and Bioresources – National Council of Research, (IGV-CNR)	Crop management, genetics, genetic resources	Gabriella Sonnante / Nicola Calabrese Via Amendola 165/a 70,126 Bari, Italy gabriella.sonnante@ibbr.cnr.it
DISAFA Plant Genetics and Breeding, University of Torino	Genetics, breeding, marker development, sequencing	Prof. Sergio Lanteri / Alberto Acquadro Largo P. Braccini 2, 10,095 Grugliasco, Torino, Italy sergio.lanteri@unito.it alberto.acquadro@unito.it
University of Catania	Crop management	Giovanni Mauromicale Via Valdisavoia 5 95123 Catania Italy g.mauromicale@unict.it
Bretagne Biotechnologie Végétale (BBV)	Biotechnology	Christophe Bazinet Pen ar Prat, 29,250 Saint Pol de Léon, France
Universidad Politécnica de Cartagena (UPCT)	Field management, stress	Prof. Juan Fernández Plaza Cronista Isidoro Valverde 30,202 Cartagena, Spain Juan.fernandez@upct.es
Universidad Miguel Hernández	Bioactive compounds	Dr. Daniel Valero Department Food Technology Ctra. Beniel KM 3.2 03312 Alicante Orihuela, Spain daniel.valero@umh.es

(continued)

Institute/Organization	Specialization research activities	Contact information and website
Instiuto Técnico y de Géstion Agricola (ITGA)	Crop management	Juan Igniacio Macua Avda. Serapio Huici 20–22 31,610 Villava. Spain
Groupe d'Etudes et de Contrôle des Variétés et des Semences (GEVES)	Seeds, clonal varieties quality	Chrystelle Jouy La Minière 78,285 Guyancourt, France
Instituto de Investigaciones en Ciencias Agrarias de Rosario (IICAR, CONICET-UNR)	Breeding, genetics	Prof Vanina Cravero Campo Experimental Villarino (S2125ZAA), Zavalla, Santa Fe, Argentina vcravero@unr.edu.ar
Big Heart Seed Company	Breeding	Nestor Rey 1280 Main Street, Brawley, CA 92227 USA rey@bigheartseed.com
Texas A&M AgriLife – Research and Extension Center at Uvalde	Crop management, organic systems, plant stress physiology	Prof. Daniel Leskovar 1619 Garner Fielf Rd., Uvalde, TX 78801, USA d-leskovar@tamu.edu

Appendix II: Genetics Resources of Globe Artichoke

Cultivar	Important traits	Cultivation location
Vegetative propagated		
Spinoso Sardo	Spiny capitula, early production	Sardinia, Liguria
Spinoso di Palermo	Spiny, average early	Palermo, Trapani, Agrigento
Violetto di Toscana	Violet capitula, spring production	Tuscany
Moretto	Violet capitula, spring production	Liguria
Castellammare	Green variegated capitula, spring production	Lazio
Catanese	Variagated capitula, early production	Sicily, Toscany, Puglia
Masedu	Variegated capitula, early production	Sardinia
Sakiz	Green variegated capitula, early production	Turkey
Bianco Tarantino	Green capitula, spring production	Puglia
Blanco de Tudela	Green capitula, early production	Spain, Argentina
Violeto de Provenza	Variegated capitula, early production	France, Italy, Algeria, Egypt

(continued)

Cultivar	Important traits	Cultivation location
Precoce di Jesi	Variegated, violet capitula, spring production	Marche
Empolese	Green variegated capitula, spring production	Tuscany
Romanesco	Violet variegated, spring production	Lazio, Argentina
Camus de Bretagne	Green capitula, spring production	France
Seed-propagated		
Imperial Star	Green capitula, spring production	USA
Opal	Variegated capitula, spring production, hybrid	Italy, Spain, Argentina, Chile
Madrigal	Green capitula, spring production, hybrid	Italy, Spain, Argentina, Chile
Deserto	Variegated capitula, spring production, hybrid	USA
Romolo	Variegated capitula, spring production, hybrid	USA

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