Apricots

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Chapter 12
Apricot

Tatyana Zhebentyayeva, Craig Ledbetter, Lorenzo Burgos, and Gerardo Llácer

Abstract Apricot is in the Rosaceae family within the genus *Prunus* L., subgenus Prunophora Focke, and the section Armeniaca (Lam.) Koch. Depending on the classification system, the number of apricot species ranges from 3 to 12. Six distinct species are usually recognized: *P. brigantina* Vill., *P. holosericeae* Batal, *P. armeniaca* L., *P. mandshurica* (Maxim), *P. sibirica* L., Japanese apricot *P. mume* (Sieb.) Sieb. & Succ. Vavilov placed apricot in three centers of origin: the Chinese center (Central and Western China), the Central Asiatic center (Afghanistan, northwest India and Pakistan, Kashmir, Tajikistan, Uzbekistan, Xinjing province in China and western Tien-Shan), and the Near-Eastern center (interior of Asia Minor). Kostina further divided the cultivated apricot according to their adaptability into four major ecogeographical groups: (1) the Central Asian group, (2) the Iran-Caucasian group, (3) the European group, and (4) the Dzhungar-Zailij group. Many local cultivars are grown in the different areas and producing countries; however, these cultivars lack important traits that needed by modern production and marketing systems. Breeding programs have and continue to develop cultivars with improved adaptability to the environment (temperature requirements, water deficit), extension of the harvest season, fruit quality for fresh consumption and processing, productivity, adequate tree size, and resistance to biotic stresses. The major objectives in apricot breeding

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programs are resistance to sharka caused by *Plum Pox Virus*, brown rot caused by *Monilinia* spp., bacterial diseases caused by *Pseudomonas* spp. and *Xanthomonas arboricola* pv. *pruni* (Smith), Chlorotic Leaf Roll Phytoplasma, and Apricot Decline Syndrome. Among these, PPV is the most limiting factor in Europe and much work has to be invested in developing PPV-resistant apricot cultivars. Molecular markers have been developed in apricot and used mainly for construction of linkage maps and genetic diversity studies.

Keywords *Prunus armeniaca* • Centers of origin • Domestication • Eco-geographical groups • Breeding goals • Breeding methods • Marker Assisted Selection • PPV resistance • Fruit quality • Inheritance • Genetic maps • Molecular markers • Genomic resources • Structural and functional genomics • Transgenics

1 Introduction

Apricot is a Rosaceae family member and belongs to section Armeniaca (Lam.) Koch in subgenus Prunophora Focke, genus *Prunus* L. (Rehder 1940). All apricot species thus studied are regular diploids, with eight pairs of chromosomes ($2n = 16$), and all can be intercrossed in either direction, making their classification confusing. Depending on the classification system, the number of apricot species ranges from 3 to 12. Six distinct species are usually recognized: Briancon apricot or Alpine plum *P. brigantina* Vill., Tibetan apricot *P. holosericeae* Batal., common apricot *P. armeniaca* L., Manchurian apricot *P. mandshurica* (Maxim), Siberian apricot *P. sibirica* L., Japanese apricot *P. mume* (Sieb.) Sieb. & Succ. (Kryukova 1989; Faust et al. 1998; Bortiri et al. 2001). Three other often recognized species *Prunus* × *dasycarpa* Ehrh., *P. armeniaca* var *ansu* (Maxim.) Kost., and *P. sibirica* var *davidiana* (Carrière) are apparently of hybrid origin. Most apricot cultivars grown for fruits belong to the species *P. armeniaca* though introgression of *P. mume* and, to the less extent *P. mandshurica* and *P. sibirica*, into cultivated germplasm is a commonly acknowledged fact among apricot breeders. Cultivation of Japanese apricot, *P. mume*, for fruit production has a much shorter history compared with its ornamental flower use (Mega et al. 1988). This review is written with emphasis on apricot species significant for fruit production.

Despite their many positive fruit attributes, namely, attractiveness, tasty flavor and ease of eating, as well as their multiple-use functionality and a nonsurplus production, apricots suffer from several weak points. As compared with the other summer fruits, apricots have a higher sensitivity to diseases. Fluctuating crop levels lead to an irregular market supply, and the narrow range of cultivars allow for only a brief market presentation. Furthermore, all too often consumers are displeased by an insufficient fruit quality and ripeness, leading to a rather low consumption rate compared to the other summer fruits (Moreau-Rio 2006; Audergon et al. 2006a).

In the last 20 years, world production has increased 85%, mainly due to the large plantings made in Asia (Turkey, Iran, Pakistan, Uzbekistan) and Africa (Algeria, Morocco, Egypt). In Europe, production increased at a lower rate, while

Table 12.1 Apricot production (MT × 1,000) from main producer countries (FAO 1989, 2008)

Country	Average production 1985–1987	Average production 2004–2006
Turkey	271	547
Iran, Islamic Republic	56	239
Italy	191	223
Pakistan	61	201
Uzbekistan	–	193
France	104	174
Algeria	40	134
Spain	148	133
Japan	–	119
Morocco	69	106
Syrian Arab Republic	57	101
China	58	86
Ukraine	–	85
Greece	112	79
South Africa	50	75
Egypt	–	73
The USA	91	65
Russian Federation	–	63
Continent		
Africa	213	437
Asia	624	1,731
Europe	745	926
Northern America	99	67
Oceania	37	21
Southern America	30	53
World	1,748	3,235

in North America and Oceania production has decreased. Near 50% of world production is concentrated in Mediterranean countries (Table 12.1; FAO 1989, 2008). The germplasm diversity that will be reported later indicates that apricots can be grown much more widely; hence the species can become a greater part of the world's fruit production. However, the limited ecological adaptation at the genotype level is the main challenge to apricot breeders. The introduction of new cultivars from foreign sources may often give disappointing results, with unpredictable variability depending on the environment (Pennone et al. 2006). Consequently, cultivars must be bred for each producing area and for each marketing opportunity (Layne et al. 1996).

The uses of apricot are multiple and diverse: fresh fruit, processed fruit for drying, canning, jam, juice, sauce, puree for baby food, wine, liquor, and vinegar (Maikeru Shoji 1994; Han 2001; Bala et al. 2005; Bassi and Audergon 2006). Traditional Chinese medicine uses bitter apricot kernels in different preparations for treating asthma and coughs, infant virus pneumonia, and disease of the large intestine (Li 1997; Chen et al. 1997). Dried fruit or fruit juice concentrate of Japanese apricot (*Prunus mume*) are used to prepare a beverage capable of preventing and

curing cancer (Fang 1995; Otsuka et al. 2005). Apricot kernel oil is used in a liquid soap composition for dermatitis treatment (Harbeck 2001). In some Asian regions, apricots used for their edible seed and seed oil are more important than apricots grown for fruit (Layne et al. 1996). The use of crushed shells of apricot stones instead of anthracite coal in filters for water treatment is investigated (Aksogan et al. 2003). The ornamental use of apricot trees is discussed later.

2 Origin and Domestication of Scion Cultivars

Some of the most significant evolutionary trends in apricot domestication have been related to fruit quality enhancement, selection of cultivars with nonbitter seeds, adaptation to a greater range of environments (i.e., development of cultivars with lower or higher chilling requirements), and a gradual change in biology of sexual propagation from self-incompatible to self-fertile.

2.1 Centers of Origin

N. Vavilov (1951) placed apricot in three centers of origin for cultivated plants (1) the Chinese center that comprises mountainous regions of Central and Western China together with the adjacent lowlands, (2) the Central Asiatic center that includes Afghanistan, northwest India and Pakistan, Kashmir, Tajikistan, Uzbekistan, Xinjing province in China and western Tien-Shan, and (3) the Near-Eastern center including the interior of Asia Minor, Transcaucasia, Iran, and Turkmenistan. After Vavilov, many discussions ensued regarding the sizes and boundaries of the proposed centers of origin (reviewed by Zeven and de Wet 1982), and in reference to apricot, it is important to mention the revision by Zhukovsky (1971), who included Turkmenistan in the Central Asiatic center and set the boundaries between the Central Asian and Near Eastern centers (Fig. 12.1).

Most contemporary authors support the antiquity of apricot in Central Asia and China and recognize them as independent centers of domestication (Bailey and Hough 1975; Kryukova 1989; Layne et al. 1996; Faust et al. 1998; Hormaza et al. 2007). However, the early history of apricot is still not completely clear. The major question whether or not its cultivation in Central Asia preceded or came after Chinese culture remains to be elucidated (Zohary and Hopf 2001). Apparently, apricot was first brought under cultivation in China. There is Chinese written evidence of apricot cultivation cited by De Candolle (1886) dating from the end of III millennium BC. In Central Asia, apricot cultivation was introduced more recently, around I–II millennia BC (Sinskaya 1969). In accordance with this dating, modern excavations in southern Turkmenistan and Uzbekistan lack evidence for use of fruit and nuts in western Central Asia before 1500 BC (Miller 1999).

In spite of a longer history of cultivation, the typical eastern cultivars did not seem to move far away from the Chinese center and remained preserved in their

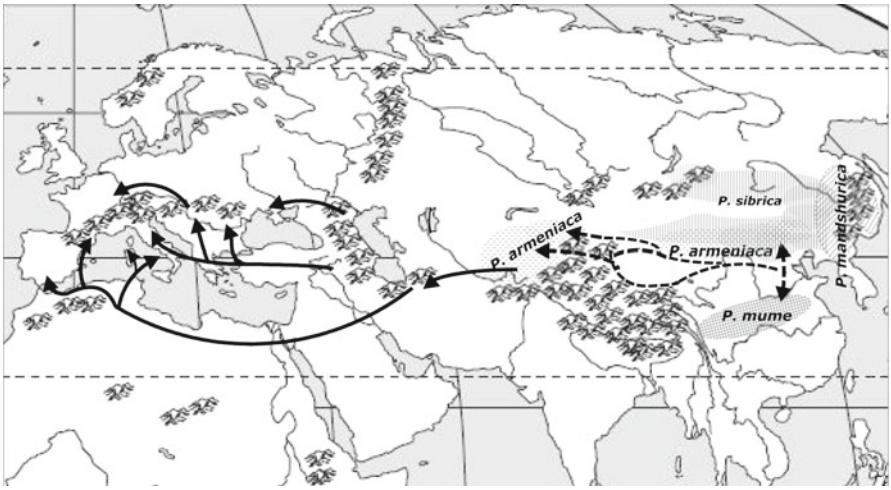

Fig. 12.1 Apricot dissemination from the primary centers of domestication (adapted from Faust et al. 1998). Outline world physical map is courtesy of Houghton Mifflin Educational Place®

native environment of Eastern Asia. It is likely that a germplasm exchange between the Chinese and Central Asian primary centers of cultivation was restricted to the first global trade route, the Silk Road, established in II–III millennia BC. Owing to the practice of seed propagation in Central Asia, the Chinese germplasm delivered through the Silk Road was assimilated and absorbed by local apricots. As a result, some aboriginal varieties grown in the Zeravshan valley and Khorezm oasis have some fruit characteristics resembling typical eastern Chinese apricots (Kovalev 1963). Molecular marker analysis supported an introgression of Chinese germplasm into the Central Asian assortment in zones of admixture linked to the Silk Road (Zhebentyayeva et al. 2003).

In studies on the origin of apricot, Kostina (1946) emphasized the importance of the Central Asian center for its spread worldwide. She definitively distinguished the apricots from Central Asia and Xinjing province in China, genetically linked to wild Tien-Shan *P. armeniaca*, from the Eastern Asian apricots related to East Asian wild species. As a result, she probably missed the Chinese group in apricot classification (Kostina 1964). A survey of indigenous Chinese germplasm (Zhao et al. 2005), as well as the noted population structure of wild apricots in the Ily valley of West China (He et al. 2007) and molecular data on crop-wide germplasm diversity (Zhebentyayeva et al. 2003), all support the theory of western Tien-Shan wild populations as being a major ancestral gene pool for apricot domestication in Central Asia and responsible for its spread from this area to more westerly regions.

In agreement with De Candolle (1886), Vavilov (1951, p. 34) and Kostina (1946) considered the Near Eastern center as a secondary center for cultivated apricots. Historically connected with China, Samarkand (Sogdiana) was the farthest reach of the Persian Empire, the Empire of Alexander the Great and the Chinese Empire. This fact was probably of critical importance for a secondary diversification of

apricot germplasm on the Iranian Plateau (Kryukova 1989). It is not surprising that a principal component analysis of 47 anatomical and morphological characteristics of the local apricots from Iran and Armenia provided evidence for involvement of both Central Asian and Chinese apricots in the development of an apricot culture in the Near Eastern center (Rostova and Sokolova 1992). Moreover, in molecular studies, Iran-Caucasian cultivars never displayed the presence of SSR alleles (Zhebentyayeva et al. 2003) or AFLP loci (Zhebentyayeva unpublished) that differ from those among Central Asian or Chinese apricots. Thus, it appears likely that the mixed germplasm arriving from Central Asia and China was adopted and further modified on the Iranian plateau.

2.2 Dissemination

Spread of apricot from its centers of first cultivation was discussed in great detail by Faust et al. (1998). In the Mediterranean basin, characteristic large apricot stones were found in several archeological sites from classical times onward (Zohary and Hopf 2001). A few hundred years later, apricot was a well-established fruit tree species in Syria, Turkey, Greece, and Italy.

Several routes have been assigned relative to the dissemination of apricot from the Near East to other regions:

1. Apricots were dispersed to the Middle East, Egypt, and North Africa, and later to Spain. This African route produced cultivars known for their low chilling requirements. Genetic structure of Tunisian apricots and their similarity to Central Asian and Iran-Caucasian apricots confirmed this dissemination route (Khadari et al. 2006).
2. A second dissemination route went north from the Black Sea, extending from Turkey or directly from Iran.
3. There was a central dissemination route to the Danube River valley and Germany. Roman soldiers and Turkish landowners were greatly involved in dissemination via this route. Probably in the Danube valley, European cultivars were originally selected for their size and adaptation to the new environment. The first forms of European apricots with mutated haplotypes conferring self-compatibility might also have originated here (Halász et al. 2007).
4. A more southerly dissemination route was assigned to Greece, and both Middle and Southern Europe, emanating north from the Mediterranean Sea. Most likely, Southern European cultivars were developed due to movement in this direction. One could consider the Italian germplasm as a secondary center of apricot diversification. In a molecular study by Geuna et al. (2003), the high level of diversification in Italian germplasm might reflect an iterative direct introgression of plant material from primary centers of origin.

The apricot spread from China and Central Asia to Europe during last 3,000–4,000 years and was subsequently taken to North America and other parts of the world. Actually, apricot arrived to North America from two opposite directions, from Europe

across the Atlantic Ocean and from China across Pacific Ocean (Faust et al. 1998). In North America, the apricot's dissemination route ended with distinct cultivars characteristic of the region: highly desirable fruit appearance (big size, orange flesh color, and firm texture), but with poor flavor and low sugar content. Perhaps due to their Chinese ancestral background, some North American cultivars developed natural resistance to a major pathogen of the *Prunus* species: plum pox virus (Zhebentyayeva et al. 2008). At the end of twentieth century, we observed the movement of North American apricot germplasm back to its Eurasian homeland for the purpose of stopping the spread of the virus in the major apricot production regions.

3 Genetic Resources

3.1 Scion

Based on a genetic approach to descriptions of morphological traits and adaptation to specific ecogeographical environments, Kostina (1936, 1964) developed a successful dichotomous classification of apricot germplasm (other classifications are reviewed in Faust et al. 1998). This classification left room for further amendments and has survived to date without major changes. Her description of diversified apricot germplasm relied on discrete qualitative traits with discrete inheritance such as seed taste (sweet/bitter), fruit skin (glabrous/pubescent), fruit adherence to stone (freestone/clingstone), fruit flesh color (orange/yellow/white), and tree architecture (upright/spreading). These oligogenic traits provided a solid framework for germplasm analysis. Quantitative traits such as chilling requirements (early/late blooming), fruit size (small/medium/large) and resistance to major diseases in specific environments along with emphasis on genetic contributions of nondomesticated species, were important for exploitation of apricot germplasm in breeding programs.

Kostina recognized four major ecogeographical groups of apricots (1) the Central Asian group with five regional subgroups: Fergana, Zeravshan, Shakhrisyabz, Khorezm, and Kopet-Dag, (2) the Iran-Caucasian group, (3) the European group subdivided for eastern, western and northern subgroups, and (4) the Dzhungar-Zailij group closely linked to the wild Tien-Shan apricot. Kovalev (1963) added the Chinese group to this classification and singled out the Southern European and North American apricots into two subgroups of European apricots. Bailey and Hough (1975) separated North African apricots from the Iran-Caucasian group, while Nyujtó and Surányi (1981) recognized only two subgroups within the European group: the continental and Mediterranean. Kryukova (1989) made the most careful revision of Kostina's classification by adding the Chinese group and incorporating the Dzhungar-Zailij apricots into the Central Asian group.

The *Chinese group* of cultivars is the oldest, the most diversified, and currently underexplored. Perhaps this group is the last world resource for apricot improvement using traditional breeding techniques. In China, six commonly accepted apricot species are endemic: *P. armeniaca*, *P. sibirica*, *P. mandshurica*, *P. holosericeae*, *P. mume*, and *P. dasycarpa*. There are also 13 subspecies of Siberian, Manchurian

and common apricots resulting from sporadic cross-hybridizations in overlapping areas (Zhao et al. 2005). More than 2,000 cultivars and life-forms have been described in China, and about one third of them are maintained at Liaoning Research Institute of Pomology, Xiongyue. The wealth of this germplasm represents the Chinese (Eastern Asian) center of apricot diversity.

In Eastern Asia, the apricot was brought under cultivation in two geographical regions (Kostina 1964; Kovalev 1963; Layne et al. 1996). *P. armeniaca* cultivars from Eastern and Central China grow in the same areas as wild *P. mume*. They adapted to a warm humid climate and developed resistance to fungal diseases. In Northern and Northeastern China, the distribution of wild *P. armeniaca* overlaps with that of *P. sibirica* and *P. mandshurica.* Northern Chinese cultivars are adapted to severe winter conditions. In molecular studies Chinese cultivars revealed their relatedness to the northeastern species *P. mandshurica* and *P. sibirica* or to *P. mume* and its interspecific hybrid with common apricot, *P. armeniaca* var *ansu* (Zhebentyayeva et al. 2003, 2008).

In China apricot production is focused on the development cultivars for fresh market, kernel production and ornamental use. The local cultivars recommended for fresh market have some individual outstanding traits, but the overall quality of these cultivars is not very good, as most of them are self-incompatible, have a short shelf life, and have limited environmental adaptation. In spite of using *P. sibirica* for apricot propagation, the fruit set and tree productivity are often low due to late season frosts. Cultivar recommendations for fresh market are as follows: early maturation season—'Luotuohuang' (earliest apricot, FDP 55 days, mean weight 51 g), 'Maihuang,' 'Hebao,' 'Shisheng'; for mid-season apricots—'Huaxiangdajiexing,' 'Shajinhong,' 'Yinxiangbai,' 'Jidanxing'; for late-season—'Chuanzhihong' (FDP 95 days, very productive, mean weight 80 g), 'Wanxing,' and 'Badou.' The best cultivar for kernel use, 'Longwangmo,' has high productivity (about 1,500 kg/ha) and seeds (~2 g) with thin shells. Apricots for ornamental use derived from the interspecific hybridization *P. armeniaca* × *P. mume* have 30–70 petals and bloom as early as *P. sibirica* 'Liaomei' and as late as *P. armeniaca* 'Shanmei' (Byrne et al. 2000).

The *Central Asian* ecogeographical group is one of oldest and richest in diversity. This group includes apricots endemic to Afghanistan, Baluchistan, Kashmir, Xinjing, Uzbekistan, Tadjikistan, Kyrgystan, and Turkmeniastan. They grow in regions that overlap with the wild Tien-Shan apricots. Owing to seed propagation and a wealth of wild germplasm, the Central Asian apricots are highly diversified. The trees are vigorous and long-lived, with an extended juvenile growth period. Most cultivars are self-incompatible. They are well adapted to a dry atmosphere and susceptible to fungal diseases.

Central Asian apricots produce fruits from small to medium in size, and without specific aroma or mealiness. The maturation season is long (from May to the end of September), perhaps the longest of the various ecogeographical groups. Skin color varies from white to intensive orange and almost red. Often fruits do not have skin pubescence. In general, the fruits have a high soluble solids content (20–30%). Acidity is usually low, in the range of 0.6–0.8% on a fresh weight basis (Kovalev

1963). Fruits are well attached and often dry (raisin) on the tree. Apricots are eaten fresh or dried. Apricot kernel production is limited to local markets.

Fergana subgroup. Apricots from the Fergana valley are of the most authentic Central Asian type (Kostina 1936; Kovalev 1963; Kryukova 1989; Rostova and Sokolova 1992). In molecular studies, this subgroup is the closest to nondomesticated *P. armeniaca* (Zhebentyayeva et al. 2003, 2008). Apricot production is predominantly for use as dry fruit. Fruits generally have a weak pubescence. There are not many glabrous cultivars (about 5%). Major cultivars of the Fergana subgroup: 'Mirsandzheli,' 'Kandak,' 'Khurmai,' 'Babai,' 'Supkhoni,' 'Isfarak,' and 'Tadzhabai.'

Zeravshan subgroup. Apricots of this subgroup grow in the Zeravshan basin (from highland to Samarkand). This group is more diversified as compared to apricots of the Fergana subgroup. Some popular landraces such as 'Arzami' and 'Akhrori' are somewhat reminiscent of Eastern Asian apricots (Kovalev 1963). Apricot production is aimed at both dried fruit and fresh market consumption. Cultivars for fresh market have an excellent fruit quality, and often open the harvest season. Occurrence of glabrous forms (lyuchaks) is high (up to 40%), and frost resistance is slightly lower than that of Fergana's apricots. Typical cultivars are as follows: glabrous forms—'Maftobi lyuchak,' 'Gulyungi lyuchak,' 'Badami'; pubescent forms—'Maftobi,' 'Gulyungi,' 'Kursadyk,' 'Khodzhendi,' 'Iskaderi,' 'Koshfi,' 'Shirpaivan.'

Shakhrisyabz subgroup. These apricots are native to Southern Uzbekistan and the Kashka-Darya basin. This group is extremely diversified and represented by cultivars for drying. As a whole, apricots of the Shakhrisyabz subgroup are small-fruited and of poor fruit quality for the fresh market.

Khorezm subgroup. The lowlands of the Amu Darya basin are the home of this Central Asian apricot subgroup. The majority of the Khorezm apricots are propagated by seed. The fruit quality is generally poor in comparison with the apricots from the Fergana and Zeravshan subgroups. However, Khorezm's apricots are more resistant to spring frosts, and can withstand both high temperatures and unfavorable soil salinity. About 10% of the cultivars in this subgroup are glabrous-skinned. Major cultivars: 'Kzyl nukul,' 'Ak nukul,' 'Kuzgi khorezmli,' 'Kzyl Khorezmskii,' 'Paivandy Bucharskii.'

Kopet-Dag subgroup. Apricots of this subgroup grow in Central and Southwestern Kopet-Dag and are characterized as being of a primitive Iran-Caucasian type. Some experts consider this semiwild population as a primary relic microcenter of the Near Eastern apricots (Avdeev 1992). However, the isozyme and DNA marker analyses support the scenario of apricot dissemination from a Central Asian center, rather than confirm the originality of this group (Zhebentyayeva et al. 2003; Zhebentyayeva and Ageeva 2004). In this subgroup, fruits are small (10–35 g) and sweet-kerneled, and have skin pubescence with a light yellow color. Taste and fruit texture are good. Kopet-Dag apricots are mainly of the fresh market type (Avdeev 1992; Kryukova 1989).

Dzhungar-Zailii subgroup. This is the youngest of the Central Asian subgroups, endemic to the most northern distribution (up to 44° north) of apricot in Dzhungar and Zailij Alatau, as well as in the Ily valley of western China. The group is comprised of the seed propagated forms selected from wild *P. armeniaca.* Cold hardiness and resistance to fluctuating winter temperatures are the most valuable characteristics of this subgroup. Generally, fruits have a light yellow color, small size and are acidic with bitter kernels. However, some forms have large fruits and are self-fertile.

The *Iran-Caucasian group* is represented by local cultivars from Armenia, Azerbaijan, Georgia, Dagestan, Iran, Iraq, Syria, and Turkey. Some Mediterranean-type cultivars in Europe have similar characteristics. Every country possesses its own germplasm resources, often the same genotypes under different names. For example, one of the best fresh market cultivars from this group is propagated under different names in Turkey ('Aprikoz,' 'Şalak') and Armenia ('Shalakh,' 'Erevani'). Generally, the apricots from this group have lower chilling requirements and bloom early in the spring. Most cultivars are self-incompatible, but self-compatible forms are not uncommon. Apricot maturation season is not as lengthy in comparison with those from the Central Asian group. The predominant fruit color is light yellow, white or creamy with sweet kernels. Glabrous-skinned fruits are rare (up to 4% cultivars).

Apricot germplasm in Turkey deserves special comment as more than 80% of the world's dried apricot originates from this region. Morphological and pomological characteristics of 128 local Anatolian cultivars provide insight on apricot germplasm of the Iran-Caucasian type (Asma and Ozturk 2005; Asma et al. 2007; Kayisi çeşit Kataloğu 1996). About one third of the Turkish cultivars bear small fruit (≤30 g). The same proportions of them have bitter kernels. Cultivars with large fruit (>50 g) are rare. Cultivars for fresh market have a high flesh to pit ratio. Prevailing fruit colors are yellow and orange, 62% and 37%, respectively. White-fleshed cultivars are rare (1%). Mid-season cultivars have high brix (>20%) that naturally contributes to high quality of the dried product. However, the fruit quality of early- and late-season varieties is poor. Major cultivars are as follows: 'Aprikoz,' 'Çataloğlu,' 'Çöloğlu,' 'Hacihaliloglu,' 'Hasanbey,' and 'Kabaaşı.'

Iran-Caucasian subgroup. Tree size and longevity of these cultivars are less as compared with those of Central Asia. However, vigorous trees with a spreading growth habit of a 'Shalakh' type (divergence angle close to 180°) occur as well. Branches are thicker with large and shiny leaves. The leaf anatomy of some typical Iran-Caucasian cultivars shares common characteristics with Chinese apricots (Rostova and Sokolova 1992).

North African subgroup Layne et al. (1996) proposed this subgroup to distinguish apricots from North Africa (Tunisia, Morocco, Libya, Algeria and Egypt). The apricots in this region grow in a climate with very mild winters and very warm summers with low rainfall. Local cultivars from this region have low chilling requirements and some have developed resistance to *Monilia* spp. (Bassi and Pirazzoli 1998). A highly likely scenario for diversification of apricots in North Africa, particularly in Tunisia, implies a bottleneck effect at the initial step of apricot cultivation followed by seed propagation (Khadari et al. 2006).

The *European group* is the best characterized of the ecogeographical groups, and is considered the youngest in origin (Kostina 1964; Layne et al. 1996; Faust et al. 1998). Under controlled propagation by grafting, practiced in Europe since its introduction, the apricot lost its variability in bloom time and maturation season, as well as other characteristics such as tree architecture. The trees are less vigorous, with open-erect growth habits, and have higher chilling requirements as compared with the Central Asia apricots. Naturalized forms of a "zherdeli" type from northern Europe can withstand very low winter temperatures while they are dormant. Most cultivars are self-compatible, but self-unfruitful varieties exist as well. European apricots, especially the newly bred varieties, have larger fruit (up to 70 g and higher) with yellow/orange color, and a characteristic apricot aroma. Glabrous forms are rare. The soluble solids content (SSC) is lower (around 12–17%) while acidity is higher (above 1.3–1.5%) compared with Central Asian varieties (Kovalev 1963; Badenes et al. 1998; Ruiz and Egea 2008). Under a Mediterranean climate, some cultivars accumulate more than 17% dry matter and are acceptable for drying. Apricot for kernel production has never been important in Europe and most cultivars have bitter kernels. It is commonly accepted that European apricots are more tolerant to fungi than Central Asian and Iran-Caucasian cultivars.

Molecular analyses of European germplasm have provided some support for diversification of the apricot in east to west direction (Hagen et al. 2002; De Vicente et al. 1998; Hormaza 2002; Geuna et al. 2003; Romero et al. 2003; Maghuly et al. 2005). Adaptation to continental or Mediterranean climatic zones was a major factor for crop evolution in European countries. The use of a few basic cultivars from clonal selection and their propagation by seedlings from open pollination led to the development of landraces of related cultivars that have a narrow genetic background and are highly specific to their ecological requirements. Apricot germplasm collections in Hungary and Italy are historically the richest in diversity and number of accessions (Zanetto et al. 2002).

By origin, commercial cultivars of North America also belong to the European ecogeographical group. Owing to the "natural" resistance to plum pox virus (PPV) uncovered in this group (for review, Martínez-Gómez et al. 2000), North American resistant cultivars were incorporated into almost all diversity studies with the use of isozymes and molecular markers (Badenes et al. 1996; De Vicente et al. 1998; Hagen et al. 2002; Hormaza 2002; Geuna et al. 2003; Romero et al. 2003). Several sources of introduced germplasm were hypothesized to explain the presence of "non-European" alleles in genotypes of PPV-resistant cultivars. More recent molecular data (Zhebentyayeva et al. 2008) provided evidence that germplasm of Chinese origin was most likely involved in diversification of North American apricots.

3.2 Rootstocks

Given the relative importance of apricot throughout the world, there is a surprisingly small amount of research and development to date for apricot specific rootstocks. Stocks have been used by growers since the discovery of grafting as a means

of saving or multiplying valuable clones. The top-working of unselected forest trees to elite selections has been practiced for centuries, and is still practiced in regions where native apricot resources exist in the wild.

Commercial canning operations and drying yards have been traditional sources of large quantities of apricot pits that could then be utilized in the production of nursery trees. While many diverse rootstock choices exist today, seedling apricot is still utilized and recommended as a first choice for new apricot orchards in various growing regions (Slingerland et al. 2002; Khadari et al. 2006). Local cultivars 'Alfred,' 'Goldcot,' 'Manchurian' and 'Veecot' were deemed the most reliable as seedling rootstocks for apricot in the growing regions surrounding Ontario, Canada. Precocity of bearing, tree longevity, and universal graft compatibility with known apricot cultivars were the reasons for the recommendation. The abundance of 'Blenheim,' 'Early Golden,' and 'Royal' pits from drying yards led Wickson (1891) to a similar recommendation for apricot seedling rootstocks in California. As the California apricot industry expanded in the first half of the twentieth century, nurseries discovered that while varieties such as 'Alexander,' 'Catherine,' and 'Tilton' produced seedlings more vigorous than those from 'Blenheim,' the 'Blenheim' variety imparted far greater vigor and longevity in the scion apricot to which it was grafted as compared with many other trialed varieties (Day 1953).

P. armeniaca is considered to be immune to root-knot (*Meloidogyne* spp.) nematode, and several studies have demonstrated its resistance to the root lesion (*Pratylenchus vulnus* Allen and Jensen) nematode as well (Day and Serr 1951; Culver et al. 1989). With resistance to these major orchard pests, one could imagine apricot rootstocks playing a major role in the production of new apricot nursery stock. However, rooting ability of both hardwood and semisoftwood cuttings is below the level of economic feasibility for commercial nurseries (Reighard et al. 1990), limiting apricot rootstocks to only those produced by seed propagation. Furthermore, graft compatibility is limited for both peach/nectarine and almond on apricot root, with specific combinations being deemed safe to producers only after empirical testing.

Besides general recommendations for use of certain varieties of apricot pits from agricultural operations, only limited research has focused on identifying superior germplasm for use as apricot rootstock. In Hungary and Bulgaria, apricot mother trees have been selected that produce seedlings with good nursery performance and broad adaptation to both pathogens and environmental problems (Mády et al. 2007; Dimitrova 2006). Specific apricot seedling rootstocks were observed to be superior by Son and Küden (2003) at imparting larger fruit size and total fruit yield in eight apricot cultivars as compared with GF 31 rootstock in Turkish orchards. In France, INRA selected and introduced 'Manicot GF 1236' as a seed propagated apricot rootstock for well-drained soils (Lichou and Audubert 1989). It is said to have very good seedling vigor and nursery homogeneity, although it is sensitive to both crown gall and bacterial canker. Seedlings from this rootstock cultivar are also susceptible to PPV (Guillet-Bellanger et al. 2006), a fact that may limit its desirability to those regions not yet affected by this important disease. Other apricot seedling populations from various 'Canino' clones have been examined as possible rootstocks for apricot. Clone Canino 9–7 yielded seedlings with higher germination and better vegetative growth than other apricot seedling populations (Orero et al. 2004).

4 Major Breeding Achievements

4.1 European Programs

Although the number of fruit cultivars available in the world is very high, there is a continuing need to develop new cultivars as industry requirements change. In the last 20 years, cultivar development by private breeding programs has increased with a corresponding decrease by publicly funded programs (Byrne 2005). In Europe, the number of breeding programs specific to apricot and new varietal releases is much lower than those focused on other fruit species. The Community Plant Variety Office (CPVO) received in 1994–2001 period over 730 new fruit cultivar applications for Community rights. Only 5% of these applications were new apricot cultivars, while new peach, apple and strawberry cultivars accounted for 20% each (Semon 2006).

The major objectives in European publicly funded apricot breeding programs are resistance to biotic stresses (sharka caused by Plum Pox Virus, brown rot caused by *Monilinia* spp., bacterial diseases caused by *Pseudomonas* spp. and *Xanthomonas arboricola* pv. *pruni* (Smith), Chlorotic Leaf Roll Phytoplasma, and Apricot Decline Syndrome), adaptability to the environment (temperature requirements, water deficit), extension of the harvest season, fruit quality for fresh consumption and for processing, productivity, and adequate tree size and structure (Bassi and Audergon 2006).

Sharka disease caused by Plum Pox Virus (PPV) is the most limiting factor for apricot production in European countries (Cambra et al. 2006a). Many of the apricot breeding programs in these countries encounter two major limitations relative to the development of new PPV-resistant varieties: PPV-resistant genitors have high chilling requirements and a medium to late harvest period (characteristics that are far from the program objectives in the southern countries), and the procedure for screening PPV resistance is a lengthy and laborious biological test involving many plants and lasting a minimum of 2 years (Badenes and Llácer 2006; Llácer et al. 2008). Taking these problems into account, it is difficult for the breeding programs in Southern European countries (Italy, France, Spain, and Greece) to reach the goal of developing new well-adapted high-quality PPV-resistant varieties.

In Italy, there are three publicly funded apricot breeding programs. The "Dipartimento di Produzione Vegetale" at Milano and Bologna Universities has recently introduced three new cultivars ('Boreale,' 'Ardore,' and 'Pieve') with better fruit quality (flavor and aroma) and an extended ripening season (Pellegrino 2006). The 'Dipartimento di Coltivazione e Difesa delle Specie Legnose' at Pisa University also recently offered three new cultivars. The first one, 'Angela,' is an early-maturing cultivar which ripens around 3 weeks before 'Canino' and a few days before 'Priana.' The second one, 'Gheriana' ripens at the same time as 'OrangeRed.' It is a cross between 'Portici' and 'Harcot,' with the best traits of both parents. The third one, 'Silvana,' is a late-maturing cultivar that ripens 25 days after 'Canino' and 10 days later than 'Fantasme.' It is a cross between 'Bergeron' and 'Canino Tardivo,' and is heavy-cropping (Guerriero et al. 2006a). Finally, the "Istituto Sperimentale per la Frutticoltura" at Caserta has produced selections that

extend the ripening season and possess interesting characteristics for specific processing products (dry fruit, canning, juice). Tests are in progress to determine the agronomic behavior of these selections in different soil and climatic conditions of southern Italy (Pennone and Abbate 2006).

In France, after a first set of 11 apricot cultivars released since 1982 for each of the three main areas of production, a new set of three cultivars has been released by CEP Innovation under the frame of a national agreement with the "Institut National de la Recherche Agronomique" (INRA) and Agri-Obtentions. 'Solédane' is adapted to Mediterranean coastal areas, 'Florilège' is suitable for the lower part of the Rhone valley, and 'Bergarouge®' Avirine is well adapted to all the French area of cultivation. The three apricot cultivars are registered in the French national catalog and protected under the UPOV rights (Audergon et al. 2006b). Some new recent selections are described by Audergon et al. (2009).

Among the main European producer countries only Spain and Greece have decreased their production in the last 20 years (Table 12.1). These countries are the most affected by PPV in the European Community (Cambra et al. 2006b; Varveri 2006). In Spain, there are two institutions that carry out apricot breeding programs aimed at producing PPV-resistant cultivars: the "Centro de Edafología y Biología Aplicada del Segura" (CEBAS-CSIC), in Murcia, and the "Instituto Valenciano de Investigaciones Agrarias" (IVIA) in Valencia. The first crosses were made in 1991 at CEBAS-CSIC and in 1993 at IVIA. The main donors of PPV resistance in these two programs were 'Stark Early Orange,' 'Goldrich,' 'Orange Red,' 'Harcot,' and 'Lito' (Badenes and Llácer 2006). The program from Murcia has already released six cultivars: 'Rojo Pasión,' 'Selene,' 'Murciana,' 'Dorada,' 'Estrella,' and 'Sublime.' The first three cultivars are PPV resistant with good fruit quality. 'Murciana' is also characterized by its good aptitude for canning. 'Dorada' is a late-ripening cultivar well adapted to the climatic conditions in the mountains of Spain (Egea et al. 2004a, b, 2005a, b, 2009). In Valencia, four varieties that fulfill the objectives of the program (PPV resistance, precocity, fruit quality, and good adaptability) are registered and 11 advanced selections are under study in several apricot regions (Martínez-Calvo et al. 2009).

In Greece, a large apricot breeding program for the control of sharka disease has been administered since 1989 at The National Agricultural Research Foundation, Pomology Institute, at Naoussa-Makedonia. Ten apricot cultivars of North American origin: 'Stark Early Orange,' 'Stella,' 'NJA2,' 'Sunglo,' 'Veecot,' 'Harlayne,' 'Henderson,' 'Goldrich,' 'OrangeRed,' and 'Early Blush,' selected for their resistance to the highly virulent local strain of PPV-M (Marcus), have been used as parents in crosses with very-high-quality cultivars, but mainly with the local cv. 'Bebecou.' Nine new apricot varieties have been introduced based on their resistance to PPV, fruit quality for fresh consumption or for canning, and other desirable characteristics (Karayiannis 2006; Karayiannis et al. 2006).

In Romania, Dr. Cociu started apricot breeding activities in 1951 within the Agronomic Research Institute in Bucharest. The main objective was to modernize the whole apricot assortment in his country. Among 29 cultivars now officially recommended for propagation and planting in Romanian orchards, 21 are new

Romanian cultivars, from which seven are early or very early and nine are later than the latest cultivar from the old assortment. They are more resistant to low winter and early spring temperatures and they have better fruit quality as expressed by size, appearance, and taste. Only six recommended cultivars are of foreign origin, and two are from the old Romanian germplasm (Cociu 2006).

In Bulgaria, a breeding program was developed at the Apricot Research Station in Silistra, with the main objective of enriching the genetic diversity in this species. Over 3,600 seedlings were obtained from 72 intraspecific crosses and 58 open pollinated cultivars. Approximately 1,300 hybrids that reached the adult phase were studied for ten important biological and pomological characteristics during 1989–1999. After a complete evaluation, nine elite genotypes, which combined the greatest number of valuable traits expressed at the highest level, were selected and recommended for cooperative trial plantings and further commercial development (Coneva 2003).

Besides PPV, apricot production in Central Europe has many risks, mainly during the postdormancy period. Particularly in these countries, the apricot decline syndrome is manifested by the emission of gum from woody organs that ends in the sudden death of branches or the apoplexy of the entire tree. Both abiotic (poor adaptation to environmental conditions) and biotic (sensitivity to different pathogens, especially bacteria and fungi) conditions seem to be the most likely causes (Bassi and Audergon 2006). These difficulties have been overcome in the breeding program initiated in 1981 at the Horticultural Faculty in Lednice, the Czech Republic. In a first generation, this program has registered seven cultivars with extended ripening times and increased frost hardiness, and another four promising cultivars have been submitted for registration. Several more hybrids with a high level of PPV tolerance have been selected for further investigation (Krska et al. 2006). On the other hand, the Research Institute of Plant Production at Piestany, Slovak Republic, has registered ten cultivars with late bloom periods, better fruit quality and extended maturation seasons (Benedikova 2006).

4.2 Non-European Programs

Outside of the European Community, numerous apricot breeding efforts have stood in regions where apricots are important, or where new apricot culture would be desirable. The oldest ongoing program for apricot improvement started in 1925 at the Nikita Botanical Gardens in Yalta, Crimea, Ukraine. Publicly funded breeding efforts exist in both New Zealand (HortResearch, Hawke's Bay, NZ) and Australia (South Australian Research and Development Industries, Loxton, South Australia) of Oceania, as well as in South Africa (Agricultural Research Council of South Africa) and Tunisia (Institut National de Recherche Agronomiques de Tunisia) of Africa, China (Liaoning Institute of Pomology, Xiongyue, Peoples Republic of China), and Japan (National Institute of Fruit Tree Science, Tsukuba, Ibaraki, Japan) of Asia, and in the USA (Rutgers University, New Brunswick, NJ and the USDA/Agricultural

Research Service, Parlier, CA). Among these breeding institutions, nearly 50 new apricot cultivars have been introduced since 1990. Numerous private apricot breeding efforts have also provided new cultivars to interested producers. With the inclusion of a recent breeding effort initiated by the University of Santiago in Chile, apricot breeding is occurring on all continents having temperate growing regions.

The development of PPV-resistant cultivars is of lesser importance to many of these programs where the virus does not pose a current threat to apricot growers. Hence, in PPV-free production regions, breeding efforts have focused on other objectives such as higher fruit quality, extended maturity season, or better environmental adaptation. The program at Yalta has had a long history of hybridization between apricots from the different ecogeographical groups with the objective being the selection of those types having high fruit quality as well as broader environmental adaptation. This hybridization scheme has been long suggested as a means of improving a cultivar's adaptation to different growing regions (Kostina 1936).

The Australian program introduced three new apricots in 2005 ('River Ruby,' 'Riverbrite' and 'Rivergold') to complement 'Rivergem,' introduced in 1995. With these new introductions, the program at Loxton hopes to revitalize the Australian drying industry. The new introductions represent marked increases in fruit quality and cropping over the industry mainstay 'Moor Park.' Furthermore, a mechanized drying industry is envisioned, with increased fruit firmness of the newer varieties now allowing experimental mechanical harvesting and cutting. Through several rounds of selection, this program has improved its overall precocity as compared with the Syrian and Turkish progenitor germplasm on which the program was originally based. Selected Chinese germplasm having novel flavors has also been incorporated into breeding lines that are adapted to the Australian growing regions. New Zealand's HortResearch program at Hawke's Bay has also been very active in variety introductions with nearly a dozen releases since 1990. 'Cluthagold' is the current top selling apricot variety, but newer releases may surpass its production as growers begin to develop new acreage. In contrast with the Australian program, HortResearch apricot development is primarily targeting the fresh market. The newer New Zealand-bred apricots have recently been dispersed to selected North American nurseries where they will be trialed.

The Agricultural Research Council of South Africa has introduced six new cultivars from their breeding effort in the last 6 years, and well over 200 advanced selections are being evaluated currently. The program has been actively importing and evaluating newly introduced apricot cultivars for their potential use as parental stock. With concern for the future, imported PPV-resistant cultivars are being bred with local adapted varieties to incorporate resistance with adaptation to the country's growing regions. In the very different environment of North Africa, Tunisian breeders have recently introduced six cultivars ('Asli,' 'Atef,' 'Fakher,' 'Meziane,' 'Ouafer,' and 'Raki') adapted to lower-chill conditions. The new cultivars show marked improvements in fruit quality (higher color, flesh firmness) over locally selected 'mesh-mesh' apricot germplasm.

Chinese breeders at the Liaoning Institute of Pomology have had several recent noteworthy achievements in expanding the apricot ripening season. Newly introduced

'Luotuohuang' is approximately 50% larger in fruit size and ripens 10 days earlier than 'Meihuang,' the previous early season industry standard. At the tail end of the Chinese ripening season, the standard cultivar 'Jinxidahongxing' has been replaced by 'Chuanzhihong,' introduced in 1997. 'Chuanzhihong' ripens 5 days later and is equal to 'Jinxidahongxing' in fruit size; however, 'Chuanzhihong' can be used as a fresh market apricot or for processing. The Liaoning Institute has also been developing apricots specifically for kernel use, with cultivars 'Fenren' and 'Guoren' both representing increased kernel size and production over the industry standard 'Longwangmao.' Liaoning Institute's newest introduction was selected from a local Chinese landrace. 'Shajinhong,' introduced in 2007, ripens mid-season and is large fruited (80–90 g), with firm flesh and very good traditional flavor/aroma characteristics. Japan's breeding effort at Tsukuba has yielded two new *P. mume* cultivars: 'Hachirou' and 'Kagajizou,' both introduced in 1997 (Yamaguchi et al. 2002a, b). The self-compatible 'Hachirou' has demonstrated a high yield of medium-sized clingstone fruit, suitable for processing into pickles. By contrast, 'Kagajizou' is pollen sterile, large fruited, and with good texture. 'Kagajizou' has been recommended for both pickling and fresh marketing.

Publicly funded apricot breeding in North America involves Rutgers University on the eastern seaboard (Cream Ridge, New Jersey) and the USDA/Agricultural Research Service in Parlier, California. The Rutgers breeding effort has achieved success in dispersing their new cultivars to both Europe and North Africa. Five new cultivars have been introduced by the Rutgers program since the mid 1990s. While not a particularly new cultivar, 'OrangeRed' (*syn*. Bhart, NJA32) has had considerable success as a fresh market apricot in medium to high chill European growing regions, and has also been used extensively as a source of resistance in developing new PPV-resistant cultivars (Karayiannis et al. 2008). 'OrangeRed' has been used as a parent in the USDA/ARS breeding effort, and is the seed parent of 'Robada' apricot. Just as with apricots from the Rutgers program, 'Robada' is being grown successfully in both France and Spain, as well as in Australia and New Zealand. Five other apricots have been introduced from the USDA/ARS program since 1994. Among them, 'Helena' (1994) has achieved considerable success in Chile as a high value fresh market export apricot. 'Apache,' released by USDA/ARS in 2001, is currently the earliest-ripening commercial apricot grown in North America.

5 Current Goals of Breeding

5.1 European Programs

This topic has been recently reviewed by Bassi and Audergon (2006). The major objectives in European programs are:

PPV resistance. PPV is the strongest obstacle for the cultivation of apricots in Europe. In the near future it will probably be impossible to grow cultivars sensitive

to PPV due to the extensive diffusion of the virus. All apricot cultivars of European origin are susceptible to PPV. Resistance has been found only in some North American cultivars. Badenes et al. (1996) were the first to suggest the role of Eastern Asiatic species, particularly *P. mandshurica*, as a potential source of PPV resistance into North American germplasm. The results from Karayiannis (2006) and Karayiannis et al. (2008) give more support to this idea, even if not all the accessions of *P. mandshurica* are PPV resistant (Rubio et al. 2003). Curiously, North American selections derived from *P. mandshurica* were introduced for their cold hardiness in midwinter and spring, late blooming and the ability to set fruit under adverse conditions for pollination (Bailey and Hough 1975). Besides *P. mandshurica*, other Eastern Asian species such as *P. sibirica* var *davidiana* and *P. mume* could also have been involved in the pedigree of PPV-resistant North American apricots. A likely scenario for introgression of resistance into North American germplasm might include hybridization of European apricots with Northern Chinese varieties cultivated in overlapping areas of *P. armeniaca* and Eastern Asian apricot species (Zhebentyayeva et al. 2008). Currently most apricot breeding programs in Europe use the PPV-resistant North American cultivars to introduce this trait into European germplasm.

Resistance to Monilinia spp. Brown rot caused by *Monilinia laxa* (Aderhold & Ruhland) Honey, *M. fructigena* Honey in Whetzel and *M. fructicola* (G. Wint.) Honey can produce notable economic damage to the apricot as well as to the other stone fruits, attacking flowers, young shoots, branches and fruits. The disease virulence and the severity of the damage are strictly related to the climatic conditions, and several fungicide treatments are often necessary to limit the damage. Therefore, the creation of new resistant varieties is one of the most important objectives of the apricot breeding programs in several European countries (Italy, France, the Czech Republic, Slovak Republic, Romania, and Bulgaria) to avoid damage to trees and yields and to reduce chemical spraying. This goal will allow reductions in both production costs and fungicide residues and will demonstrate a better respect for the environment. In Italy, a breeding program for *M. laxa* resistance reported 11 advanced selections that were evaluated as resistant to the damaging fungus (Nicotra et al. 2006).

Resistance to bacterial diseases. The bacterial diseases in apricot are mainly caused by *Pseudomonas* spp. (wood cankers) and *Xanthomonas arboricola* pv. *pruni* (Smith) (leaf necrosis). The spreading of the first pathogen is facilitated by cold winters and humid climates. The lesions produced by exposure to cold temperatures can be easily infected and develop cankers that may lead to loss of branches, scaffolds or even of the whole tree. *Pseudomonas syringae* pv. *syringae* van Hall along with the fungus *Leucostoma cincta* (Fr.:Fr.) Höhn and winter injury are the major contributors to apricot decline or apoplexy syndrome in central Europe (Layne et al. 1996). *Prunus dasycarpa* sel. P 2315 and the Japanese apricot (*P. mume*) have been described as immune or highly resistant to *Pseudomonas* spp. On the other hand, *X. arboricola* pv. *pruni* spreads in warm and humid climates and affects shoots,

leaves and fruits. The cultivars 'Adedi,' 'Alfred,' 'Polonais,' and 'Tirynthos' are recorded as tolerant or not very sensitive to leaf necrosis. Selection can be made for tolerance by artificial inoculation methods on progenies from crosses with highly tolerant parents.

Resistance to Apricot Chlorotic Leaf Roll (*ACLR*). ACLR is caused by European Stone Fruit Yellows Phytoplasma. It produces a progressive decline of the tree due to obstruction of the vessels. It is transmitted by grafting and some insects, and its diffusion is very serious in Southern France. Some tolerant sources are known that develop symptoms only after a prolonged time period after infection. No sources of immunity are known.

Adaptability to the environment. This trait is still one of the main factors limiting a cultivar's introduction outside the environment where it was selected. The temperature regime during summertime can affect bud flower differentiation and during the winter can alter the morphological completion of the ovary. Another aspect is the sensitivity to spring frosts. This sensitivity cannot only be attributed to early blooming. In experiments carried out in northern Italy (Bassi et al. 1995), it was shown that the early blooming genotypes are not always less productive than those with middle or late blooming times. These genotypes are characterized by very abundant bloom, a phenomenon that often compensates for the effects of late frosts. Parents with spring frost tolerance in apricot and the use of artificial cold-stress methods, eliminating the multiple variables of the field, have been described by Guerriero et al. (2006b).

On the other hand, the tendency to search for genotypes with late blooming time may lead to the introduction of cultivars characterized by high chilling requirements, difficult to satisfy in regions with mild winters. Better results can be obtained by breeding genotypes with high heat requirements, which causes late blooming without negative effects. The cultivars adapted to northern environments show very poor growth with scarce floral induction when grown in mild conditions. This is the problem for southern European countries when using North American genotypes to introduce PPV resistance.

Another phenomenon in terms of adaptation is fruit cracking. While there is certainly a genetic predisposition in specific apricot cultivars, fruit cracking is also strongly dependent on the tree's water balance when the fruit is close to maturity. Rain during this stage, especially when following a dry period, causes an abundant absorption of water by the fruit which can then crack the skin or even split the mesocarp. Among the tolerant cultivars in Italy or France are 'Boreale,' 'Fournes,' 'Goldrich,' 'Moniquí,' and 'San Castrese.'

Extension of the ripening time. In all apricot-producing areas, a frequent goal is the extension of the ripening season to allow better packing house use efficiency and a larger presence in the marketplace. Moreover, earlier and later harvested fruits are often marketed with higher prices (Llácer 2009). There are many potentially useful genotypes for extending the ripening season. Concerning a very early ripening time, there are germplasm resources from Mexico (Pérez-González personal communication), from northern Africa and selections from the program at Rutgers University

(the USA), ripening 11–18 days before 'Tyrinthos.' These genotypes were obtained from progenies using American cold resistant cultivars crossed with high fruit quality Central Asian germplasm. Considering the great genetic diversity between the parents, this germplasm can be outstanding breeding stock for future crosses. In relation to late ripening, many potentially interesting parents are also available: 'Reale di Imola,' 'Boccuccia Spinosa,' 'Baracca,' 'San Francesco,' 'Fracasso,' and 'Pisana' from Italy, 'Bergeron' and 'Tardif de Bordaneil' from France, and many of the Eastern European and middle-Asian genotypes. All this germplasm, however, shows lack of adaptation outside its place of origin and some poor traits related to late ripening.

Fruit quality. All cultivar programs point out fruit quality as a priority, but this is a complex trait that needs to be defined for every situation and use. Sensory fruit quality concerns consumer perception of color, shape, size, aroma, flavor, texture, and freshness. There is an external fruit quality, which is perceived by sight, and an internal fruit quality where perception occurs during fruit consumption (Llácer 2009). External fruit quality has been a priority in the past. Owing to consumer preferences, this trend is changing and the internal fruit quality is becoming a priority goal. The lack of internal fruit quality is the main reason claimed by consumers for buying less fresh fruits (Byrne 2002). Additionally, nutritional quality, the content of polyphenols and carotenoids, and food safety are becoming important factors in determining the level of fruit consumption (Ruiz et al. 2005; Badenes et al. 2006). Other traits are also important both for field and postharvest operations: the uniformity and speed of ripening, resistance to handling and transportation, sensitivity to internal browning and adhesion to the pit. For canning apricots, good orange skin and flesh are desired, as well as a uniform medium size, regular shape, resistance to pit burn during high temperatures just before harvest, good texture (freedom from fibers and vascular bundles), small pit, high sugar content, and a good balance of acid and sugar (Layne et al. 1996). For drying, subacid fruits (acidity lower than 0.5%) with high soluble solids (20–25% of sugar) are needed. In general, it can be said that the objectives of the different processing destinations, being rather specific, can be easily achieved by traditional breeding programs, although most of the important traits are quantitatively inherited.

Productivity. This is a basic goal in any breeding program. From a purely economic viewpoint, a consistently productive cultivar of medium fruit quality is generally more profitable in comparison to a high-quality cultivar prone to alternate yields. Productivity depends on several factors: the adaptability to the environment (discussed above), the proportion of normally differentiated flowers and the self-compatibility status of the tree. A rather high percentage of self-incompatible genotypes exist in cultivated apricots. The need for reliable pollinizers to avoid erratic fruit set in these types of apricot cultivars was emphasized by Rodrigo and Herrero (1996). It is very important to carefully evaluate the floral compatibility before introducing a new cultivar, keeping in mind that it would be very difficult to evaluate this trait in a cultivar collection where many pollinizers are usually available. The use of molecular markers has greatly facilitated the identification of self-(in)compatible genotypes, as will be discussed later.

Tree size and structure. Presently, the integration of morphological and architectural traits in fruit tree breeding programs is an important goal in France and Italy. The use of small stature trees as parents could result in progenies characterized by short internodes, fruiting branches and/or spurs (Moser et al. 1999). In many genotypes the fruits obtained from spurs are of better quality than those obtained from standard branches. On the other hand, apricot trees are not very adaptable to formal or rigid training systems and they do not tolerate drastic pruning, particularly in the dormant season. Consequently, it is important to develop tree forms that require infrequent management of the vegetation while producing consistent and adequate yields. A review of these traits has been presented by Costes et al. (2004).

Adaptability to various soil conditions. A large genetic diversity of rootstocks used for apricot is employed in Europe, depending on the various soil conditions of growing areas. Apricot, peach and plum seedlings, clones of different plum species or interspecific hybrids are currently used in apricot orchards. Nevertheless, graft incompatibility, exhibited by many *Prunus* rootstocks with most apricot cultivars, is one of the major problems for rootstock usage and improvement. Interspecific hybridizations between myrobalan plum (*P. cerasifera*) and apricot (*P. armeniaca*) have been undertaken in France and Spain to create hybrids that combine graft compatibility with apricot, favorable rootstock traits from myrobalan plum (adaptation to heavy soils, rooting ability) and resistance to pests and diseases from both species. The first results obtained show that the creation and selection of these interspecific hybrids seems to be a very promising way to improve apricot rootstocks (Poëssel et al. 2006; Arbeloa et al. 2003, 2006).

5.2 Non-European Programs

The lack of PPV in California orchards has allowed the USDA/ARS breeding program to focus effort on specific fruit quality characteristics. Repeat consumer sales throughout the apricot marketing season are hurt by the abundance of low quality (immature, high acidity, low Brix) fruit during the early season. In order to increase the overall fruit quality, numerous California adapted apricots have been hybridized with apricots from Central Asia (Ledbetter and Peterson 2004). The use of Central Asian parents added a great deal of genetic diversity to the program. Novel and useful characteristics obtained from Central Asian parents include late bloom period, high Brix, long fruit development period, glabrous skin, modified sugar profile and diverse skin and flesh colors. The USDA/ARS breeding goals involve new cultivar development for the fresh and processing markets. The expansion of the fruit maturity season is an overall goal, with the current season being only 5 weeks. Numerous crosses have been made to incorporate glabrous skin into California adapted apricots. White flesh apricots are being selected for flesh firmness and high Brix. For processing apricots, the major emphasis is in identifying high Brix freestone drying types whose flesh color will not darken in storage after sulfur/sun drying. At the Rutgers University breeding program, improved cold hardiness is a major goal as inclement springtime weather conditions can limit apricot production. Like the

USDA/ARS program, Rutgers' breeders are actively selecting for high fruit quality and attractiveness, and to lengthen the ripening season. Cream colored flesh and glabrous skin are two novel characters currently under selection at Rutgers.

The breeding work at Tsukuba, Japan has goals for both *P. armeniaca* and *P. mume*. Objectives for Japanese apricots are focused on the fruit's processing ability into "pickles," with particular importance being placed on low gumming of the fruit. Selections are made for a later flowering season and early fruit maturity is desirable as well. Plum × *P. mume* hybrids are also being evaluated for juice and liquor production. Pigments in the hybrid flesh impart a bright red color to products produced from them, providing novel and potential value-added benefits. The Tsukuba team's goals for *P. armeniaca* selections are very low acidity and high Brix in apricots for the fresh market. Tree longevity is desirable, as is a late bloom period, given the propensity of late frosts throughout the Japanese growing regions. Self-fruitfulness and disease resistance are breeding goals in both *P. armeniaca* and *P. mume*. Having a series of sequentially ripening apricots with abundant flavor and firm flesh is the overall goal of the Chinese breeders at Liaoning Institute. To achieve this goal, numerous firm-fleshed North American apricots have been imported for evaluation and for hybridizations with local Chinese landraces having strong aroma/flavor. Future selections will be made where these important traits are combined throughout the fruit maturity season (Weisheng Liu personal communication).

Tunisia's geographic location provides the potential for having available apricots in the earliest possible season, given the availability of adapted germplasm. Breeders at the Institut National de Recherche Agronomiques de Tunis have endeavored to combine several fruit quality traits (orange color, firm flesh, large fruit size, enhanced sugar and aroma) with early-ripening, hoping to produce export-quality cultivars that are ready for harvest and marketing prior to when the first European Community apricots are ready. The Agricultural Research Council of South Africa is evaluating apricot selections for both fresh marketing and processing potentials. With exportable fruit being an important percentage of South Africa's apricot tonnage, postharvest cold storage ability is one of the major breeding objectives. The program continues to import, under quarantine, high fruit quality and PPV-resistant cultivars from other breeding programs for use in hybridizations with locally adapted selections. Thus, this program demonstrates forethought in their breeding goals relative to the nearly inevitable future introduction of PPV into South African growing regions.

New Zealand's HortResearch breeding program desires to develop well-adapted and precocious cultivars that are productive, large-fruited and have both good eating quality and high flavor. Breeders there are also attempting to develop early maturing cultivars for the Hawke's Bay growing region (lower chill area) and late maturing cultivars for the growing regions of Central Otago (higher chill area). A more immediate goal for HortResearch breeders is the replacement of the 'Sundrop' cultivar, an industry standard for both growing regions, due to both cropping concerns and insufficient fruit size (Mike Malone personal communication). Similar breeding objectives exist for the program at Loxton, South Australia; however, Australian breeders are selecting apricots for the drying and processing markets as well as for

fresh fruit. With similarities to the program in South Africa, postharvest researchers are assisting in the evaluation of elite fresh market selections to identify those most suitable for export marketing. In addition to high Brix and good product color in dried apricots, Australian breeders aim to automate their drying industry by supplying new cultivars capable of mechanical harvest and fruit cutting, and with low drying ratios.

6 Breeding Methods and Techniques

6.1 Genetics

Breeders generally agree that most apricot traits are quantitative, suggesting a polygenic inheritance (Table 12.2). Although only a few inheritance studies have been done on apricot traits, the high or very high heritability values of most of the traits studied indicate the suitability of choosing parents based on their phenotype and also the high potential for genetic improvement in this species (Couranjou 1995). Crosses made between Asian and European genotypes suggested that traits from the Asian group such as small fruit, large pit, high soluble solids content, long dormancy period and late flowering season have dominant inheritance, while the complementary traits from the European groups are recessive. Similarly, results from crosses between Iran-Caucasian and European apricots suggested that flesh and skin color, and extent of red blush on the fruit are independently inherited (Badenes et al. 2006).

Table 12.2 Quantitative traits suggesting a polygenic inheritance

Trait	Reference
Flowering date	Couranjou (1995)
Maturity date	Couranjou (1995)
Yield	Couranjou (1995)
Fruit size	Couranjou (1995)
Fruit weight	Signoret et al. (2004), Chen et al. (2006)
Fruit skin background color	Couranjou (1995)
Flesh color	Couranjou (1995)
Skin overcolor	Couranjou (1995)
Fruit firmness	Couranjou (1995), Signoret et al. (2004), Peace et al. (2007)
Fruit flavor	Couranjou (1995)
Fruit aroma	Couranjou (1995)
Fruit juiciness	Couranjou (1995)
Self-pollinated fruiting rate	Chen et al. (2006)
Fertile flower rate	Chen et al. (2006)
Fruit sugar content	Signoret et al. (2004)
Fruit acid content	Signoret et al. (2004)
Resistance to *Monilinia laxa*	Conte et al. (2004), Nicotra et al. (2006)

Ripening of climacteric fruits is a complex process that includes many changes in gene expression, especially for enzymes involved in cell wall modifications. Two expansion cDNAs from apricot expressed during fruit ripening are each regulated differently by ethylene (Mbeguie et al. 2002; Mita et al. 2006). Ethylene also regulates the carotenoid accumulation and the carotenogenic gene expression in apricot varieties (Marty et al. 2005; Kita et al. 2007). In peach, Peace et al. (2005) identified endopolygalacturonase (endoPG) as the gene controlling the major fruit firmness and texture traits. Given the close synteny within *Prunus*, endoPG may play a similar role in apricot (Peace et al. 2007).

Regarding resistance to *Monilinia laxa*, the results from Nicotra et al. (2006) indicate that the characteristics "branch resistance" and "fruit resistance" are controlled by different genes, without correlation between them.

The inheritance of chilling requirement for dormancy completion in apricot was studied by Tzonev and Erez (2003). They concluded that this characteristic represents two distinct genetically controlled traits, the first one is a "switch" for bud break and the second is the vigor of the ensuing bud growth. In terms of the inheritance patterns for these traits, low chilling seems to be dominant over high chilling, whereas the second trait exhibits a nondominant intermediate response between the parents.

Some traits inherited in a discrete manner, suggesting an oligogenic inheritance pattern, are seed bitterness (Gómez et al. 1998), male sterility (Burgos and Ledbetter 1994), self-incompatibility (Burgos et al. 1997, 1998), and PPV resistance (Karayiannis et al. 2008).

6.2 *Breeding Strategies*

Intraspecific hybridization is the most widespread method for apricot scion breeding, while interspecific crossing between *Prunus* species is common for rootstocks breeding or for novel trait improvement in scion cultivars (Bassi and Audergon 2006). For very old cultivars (especially those locally propagated by seeds), screening their natural variability could lead to the selection of improved phenotypes (clonal selection). Physical mutagenesis with gamma-rays or ^{60}Co has been used to increase variability in apricot (Legave and Garcia 1988; Balan et al. 2006), while in vitro cultured anthers were utilized to produce haploid plants (Peixe et al. 2004).

Given a long juvenile period and large plant size, the cost of growing each seedling is high and consequently, when planning a breeding program it is very important to clearly define the objectives, carefully select the parents and specifically define the selection criteria accordingly. Seedling evaluation is based on a two-stage procedure (1) observation of the hybrid on its own roots during 3 consecutive years of production and (2) evaluation of the best hybrids after grafting in several representative areas of production during 3 consecutive years. Considering the juvenile periods in the two stages, the length of the breeding cycle is at least of 12 years. A third stage for assessment of the agronomic and commercial interest of the "elite" hybrids in precommercial orchards is often carried out, particularly in public programs (Audergon et al. 2009; Llácer 2007).

The hybridization techniques (pollination, seed handling, and seedling evaluation) have been extensively described by Layne et al. (1996). However, some improvements can be reported. Mistakes in assigning seedling paternity are more frequent than it seems. When there is a period of cool weather during the blooming season the anthers of some cultivars may dehisce before the petals open. In controlled crosses, when using a self-compatible female parent, all or part of the seedlings may not come from the cross but they may come from selfing (Llácer et al. 2008). Likewise, the incidence of accidental pollination with undesired pollen on interspecific hybridizations was studied by Arbeloa et al. (2006). The percentage of desired hybrids was lower than expected. In these situations, molecular characterization of the progeny should be carried out for paternity assessment.

Regarding seed handling, apricot embryos (seed-coat removed) stratified for 15 days at 4°C have higher germination percentages and seedling growth than those stratified by the standard procedure (pits stratified at 4°C for 2–3 months). This procedure allows plants to get ready for testing (PPV or other pathogen resistance) as soon as possible (Badenes et al. 2000). Embryo culture in vitro can be successfully used as a tool in an apricot breeding program to obtain higher percentages of seedlings or to overcome a lack of seed germination, as occurs with very early-ripening female parents that may not have fully mature embryos (Burgos and Ledbetter 1993; Arbeloa et al. 2003).

Relative to seedling evaluation, methods of screening for resistance to *Monilinia* spp. (Walter et al. 2004) and to PPV (Karayiannis et al. 2008; Llácer et al. 2008) have been recently reported.

The most important progress has been achieved in determination of fruit chemical profiles. High-performance liquid chromatography (HPLC) combined with other identification methods have been applied to the evaluation of vitamins, selenium, carotenoids, polyphenols, and total antioxidant capacity (Munzuroglu et al. 2003; Radi et al. 2004; Veberic and Stampar 2005; Scalzo et al. 2005; Dragovic-Uzelac et al. 2007). Cyanogenic glycosides have been analyzed by HPLC in sweet and bitter kernelled apricot varieties in relation to the resistance to *Capnodis tenebrionis* L. (Sefer et al. 2006).

Near (NIR) and middle (MIR) infrared reflectance spectroscopy have been used for the rapid determination of fruit quality traits such as soluble solids content and titratable acidity (Bureau et al. 2006), while headspace-solid phase microextraction combined with gas chromatography–olfactometry has been applied for aroma characterization (Guillot et al. 2006).

7 New Biotechnology Techniques Available for Fruit Breeding

Traditional fruit tree breeding is a time consuming process in which progress is dependent on a favorable environment during the annual bloom period. Implementation of molecular markers linked to traits of interest, is a direct way to accelerate new cultivar development in deciduous plants with a long juvenile period. Discovery of the nearly complete synteny of genetic linkage maps between *Prunus*

species was the major achievement in the area of fruit tree genetics that led to recognizing genomes of all diploid species, including apricot, as a single genetic entity (Arús et al. 2006). This new vision of the *Prunus* genome organization will have an impact on all areas of fruit tree research from classical botany (how many distinct species?) to a modern transgenic study (why are all diploid *Prunus* species so tough to transform?).

A saturated reference map for *Prunus* (Dirlewanger et al. 2004), further enriched with bin mapped markers (Howad et al. 2005), allows an easy transmission of the genetic and genomic information across the genera, i.e., in-between apricot and peach, almond, diploid plums, or cherry. The recent development of centralized bioinformatics resources, Genome Database for Rosaceae (GDR), facilitates this process (Jung et al. 2008). GDR is a major repository of curated and integrated genetics and genomics data of Rosaceae that contains annotated databases of all publicly available *Prunus* ESTs (Expressed Sequence Tags), including those derived from the apricot fruit and leaf cDNA libraries. A genetically anchored peach physical map, apricot genetic maps and comprehensively annotated markers and traits will enable the acceleration of a comparative map of complex traits, and support map-based cloning genes of horticultural importance in apricot (Fig. 12.2).

7.1 Molecular Markers Available for Breeding in Apricot

In apricot, molecular markers were employed for cultivar fingerprinting and to evaluate variability across the crop, for construction of molecular genetic maps, and to develop markers for parental analysis and marker-assisted breeding (complementary review by Hormaza et al. 2007). The list of markers includes isozymes, Randomly Amplified Polymorphic DNAs (RAPDs), Restriction Fragment Length Polymorphisms (RFLPs), Amplified Fragment Length Polymorphisms (AFLP) and Simple Sequence Repeats (SSRs). More sophisticated marker systems include AFLP markers targeting the Resistance Gene Analogs (AFLP-RGAs) or differently expressed cDNAs (AFLP-cDNA), candidate genes for particular traits such as self-incompatibility and resistance to PPV, and EST-SSRs, the SSR markers from the annotated EST (Expressed Sequence Tag) database.

Isozymes, *RAPDs*, *RFLPs*, *SSRs.* The first publications on isozyme analyses in apricot are attributed to Byrne and Littleton (1989). Based on mean heterozygosity at 10 isozyme loci and mixed mating system, apricot was considered as a suitable crop for diversity studies (Byrne 1990). In spite of the limited number of loci, isozymes proved to be reliable markers for genetic variability assessment (Badenes et al. 1996) and cultivar identification (Zhebentyayeva et al. 2001). In a short time, isozymes were replaced with more efficient DNA based markers such as RAPDs (Gogorcena and Parfitt 1994; Takeda et al. 1998; Mariniello et al. 2002), RFLPs (de Vicente et al. 1998) and SSRs (Hormaza 2002; Romero et al. 2003; Zhebentyayeva et al. 2003; Krichen et al. 2006; He et al. 2007). Owing to dominant inheritance and low reproducibility, the application of RAPD markers was limited

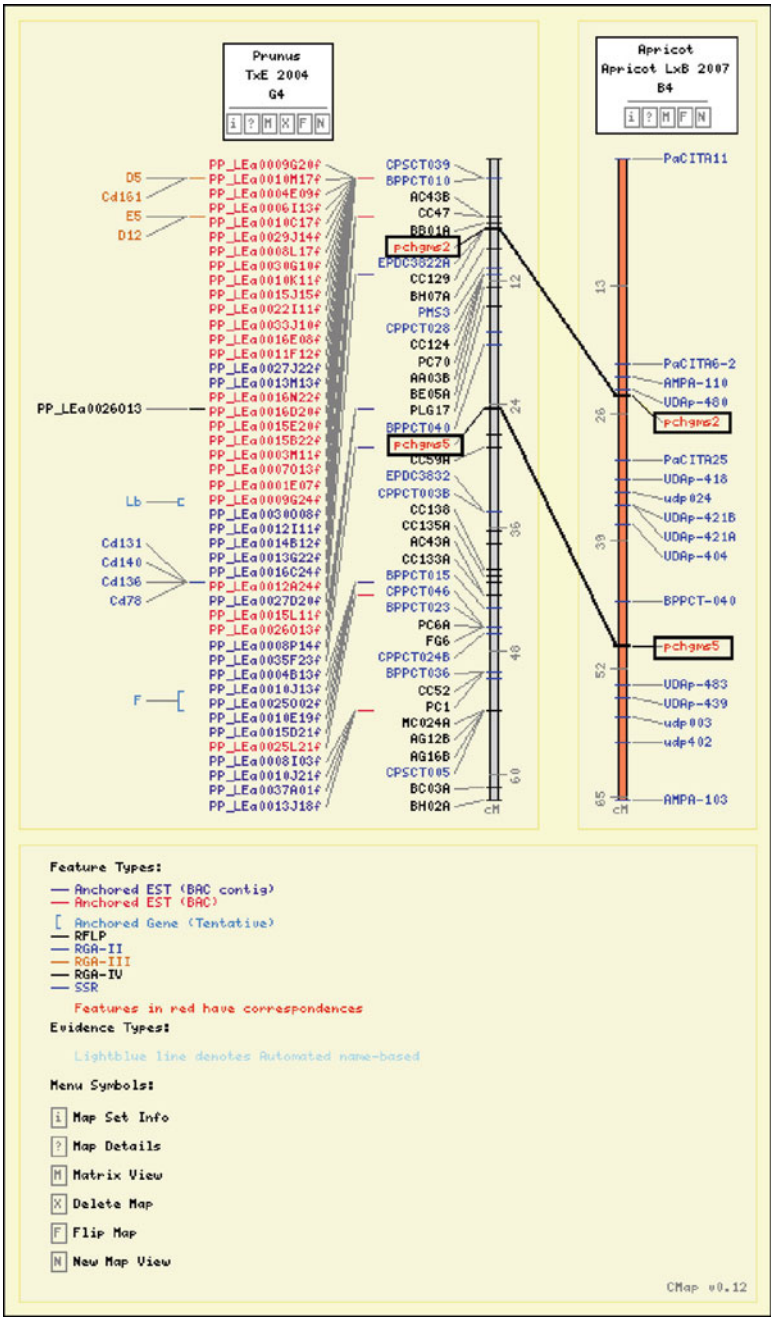

Fig. 12.2 CMap alignment using GDR tools. A screenshot of a CMap page that shows the comparison between G4 of the *Prunus* map and male parent BO81604311 of the apricot L×B map by Dondini et al. (2007). The peach ESTs (PP_LEa), candidate genes representing of RGAs (Cd) and the anchored trait positions are shown on the left. Two SSR loci pchgms2 and pchgms5 (in *boxes*) were used for alignment between two maps

to several publications. Codominant RFLP markers have also not found a broad application because they are not cost-effective, demanding in terms of DNA quality and tedious in execution. PCR-based and amenable to automation, codominant SSRs became the markers of choice in germplasm analysis and cultivar fingerprinting. Semiautomated genotyping of 132 cultivars using high-throughput capillary electrophoresis has been reported recently (Maghuly et al. 2005).

AFLPs. In spite of their dominant inheritance, AFLP markers provide reliable diagnostic loci at varying taxonomic levels. Numerous AFLP markers could be easily generated for many applications. They were used for analysis of diversified germplasm from different ecogeographical group and nondomesticated species (Hurtado et al. 2002a; Hagen et al. 2002), for investigation of genetic structure in Tunisian apricots (Khadari et al. 2006) and for purpose of cultivar fingerprinting (Geuna et al. 2003). Diagnostic AFLP loci along with targeted SSR markers provided more insight on potential origin and breeding history of the PPV-resistant North American apricots (Zhebentyayeva et al. 2008). AFLP markers were successfully applied for germplasm analysis in Japanese apricot (*P. mume*) and in relation to their origin and dissemination from the southwest of China (Yang et al. 2008). So far, six of seven published genetic linkage maps were saturated with AFLP markers (Table 12.3). The application of an AFLP technique to bulks made of PPV susceptible and PPV-resistant individuals initiated a BAC-based development of PPV targeted SSR markers for segregation analysis and MAS (Lalli et al. 2008).

Advanced marker systems. A shift from random marker systems to markers of a known genetic location on a *Prunus* map, or based on sequences with known functions is the most recent trend in the development of marker systems in apricot and other species.

Taking advantage of a domain conservation across the families of RGAs, Soriano et al. (2005) characterized 43 unique RGA sequences from PPV-resistant genotypes and developed 27 AFLP-RGAs markers for mapping in the apricot F_2 population Lito×Lito (Vilanova et al. 2003b). Alternatively, analogs of virus resistant genes from apricot were positioned on F_1 and F_2 maps of *P. davidiana* (Decroocq et al. 2005) or localized on integrated peach physical/genetic map (Lalli et al. 2005).

Gene-derived EST-SSRs, in contrast to SSRs generated from genomic libraries, are associated with coding sequences within genomes and provide functional information for downstream applications. Thus far 180 gene-derived EST-SSRs were identified among peach and almond ESTs (Expressed sequence tags) (Jung et al. 2005) and 21 SSRs were isolated from apricot fruit ESTs and cDNA sequences (Decroocq et al. 2003; Hagen et al. 2004). Generally, expressed sequences have proven to be an efficient source of polymorphic SSR markers to facilitate candidate gene approach for genetic mapping and map-based cloning. The list of SSR markers identified in *Prunus* EST Unigene_v4 and primer sequences automatically designed using GDR tools are available at: http://www.bioinfo.wsu.edu/gdr/projects/prunus/unigeneV4/downloads/PrunusContigsV4_SSR_ORF_PRIMER.xls.

Table 12.3 List of the published apricot maps

Cross	Progeny	Markers (total); trait	Parent and average distance (cM)	Reference
Goldrich × Valenciano (F1 G × C map)	81	AFLP, RAPD,RFLP, SSR (132); PPV	Goldrich-511 Valenciano-467	Hurtado et al. (2002b) (First generation map)
Lito × Lito (F2 L × L map)	76	AFLP, SSR (211); PPV, self-incompatibility	602	Vilanova et al. (2003b) (First generation map)
Polonais × SEO (F1 P × S map)	142	AFLP, RFLP,SSR, cDNA-SSR (141); PPV	Polonaise-538 SEO-699	Lambert et al. (2004, 2007)
Lito × Lito (F2 L × L map)	76	AFLP, SSR, AFLP-RGA (231); PPV, self-incompatibility	615	Soriano et al. 2008 (Second generation map)
Goldrich × Currot (F1 G × C map)	81	AFLP, RAPD,RFLP, SSR (139); PPV	Goldrich-468 Valenciano-451	Soriano et al. (2008) (Second generation map)
LE3246 [SEO × Vestar] × Vestar (BC1 LE × V map)	67	AFLP, SSR (357); PPV	523	Lalli et al. (2008)
Lito × BO81604311 (F1 L × BO map)	125	SSR (185)	Lito-504 BO81604311-620	Dondini et al. (2007)

7.2 State of the Maps

Resistance to PPV was a major focus in all mapping projects published to date. Complete maps were generated for five segregating crosses and, currently, the PPV resistance trait is mapped in four of them: 'Goldrich' × 'Valenciano' (syn. 'Currot'), 'Lito' × 'Lito,' 'Polonais' × 'Stark Early Orange,' (SEO) and LE3246 × 'Vestar' (Table 12.3). Two of the listed maps, 'Lito' × BO81604311 (Dondini et al. 2007) and 'Polonais' × 'SEO' by Lambert et al. (2004) were established using the codominant markers only. Apricot maps are organized in eight linkage groups. The reported total lengths of approximately 500–600 cM are close to that of the *Prunus* map. The mean densities of markers are about 2–4 cM. The highest marker density of 0.92 cM was obtained in G1 on LE3246 × 'Vestar' map (Lalli et al. 2008).

Self-incompatibility and PPV resistance are two traits positioned on the apricot maps. The self-incompatibility locus was located at the end of G6 in agreement with the *Prunus* map. Mapping of PPV resistance is still underway (Hurtado et al. 2002b; Vilanova et al. 2003b) and its control is not completely understood, mainly due to trait complexity and differences in phenotype scoring. The most comprehensive discussions on testing different hypotheses for control of PPV resistance were reported recently (Rubio et al. 2007; Karayiannis et al. 2008; Sicard et al. 2008; Soriano et al. 2008; Lambert et al. 2007; Lalli et al. 2008). At least one genetic location in the upper part of G1 found consensus across the mapping community and was accepted as the major locus conferring the dominant resistance to PPV. On the G × V, L × L, and P × S maps, resolution of the G1 region was increased by mapping PCR-based markers derived from apricot candidate genes potentially involved in resistance to virus (Sicard et al. 2008). Two additional putative QTL loci, including the one detected during the early stages of infection, were localized in the P × S population on G3 of 'Polonais' and G5 of both 'Polonais' and 'SEO' (Lambert et al. 2007).

7.3 Marker-Assisted Selection

Marker-assisted selection (MAS) is the most efficient application of molecular tools and markers to improve apricot cultivars using traditional hybridization techniques. This is especially true in the case of interspecific crosses, when desirable fruit quality often appears as early as a second backcross generation.

Owing to the high level of synteny, markers linked to simple horticultural traits such as fruit color, nonacidic fruit taste, glabrous skin, sweet kernel, and stone adherence can be easily verified and adopted across all *Prunus* species. The same is true for qualitative traits such as bloom time, ripening period, and fruit quality characteristics (Dirlewanger et al. 2004).

Breeding for PPV-resistant cultivars. Evaluation of PPV resistance is the major limitation for apricot breeding programs in many countries. Generational genetic

linkage maps for crosses segregating for PPV resistance have located several markers on G1 that were potentially useful in breeding programs. Associations with PPV resistance were reported for markers ssrPaCITA5 and ssrPaCITA17 in Soriano et al. (2008), aprigms18 and EPDCU5100 in Lalli et al. (2008), and pchcms4, RFLP marker AG51, AFLP E37-M13-208 in Lambert et al. (2007). The four markers cd83SSR, cd93SSR, cd195SSR, and cd211SSR were developed with genes potentially involved in plant–virus interactions in Sicard et al. (2008). Altogether, 11 markers are potential candidates for the use of MAS in breeding. Three of them (ssrPaCITA5, ssrPaCITA 17, and aprigms18) were tested for MAS in several crosses from the breeding program at IVIA, Valencia, Spain (Soriano et al. 2008). Depending on the particular population, the proportion of misclassified susceptible seedlings varied from 40 to 69%, while more than 90% of the most resistant plants were preserved in F_1 and F_2 progenies. Further saturation of the PPV resistance region is needed to improve the efficiency of MAS for this trait.

Breeding for self-compatibility. Self-incompatibility (SI) in apricot is another important target for the application molecular technologies. Theoretical background and proposed mechanisms for gametophytic SI (GSI) that apricot shares with other Rosaceae species is thoroughly reviewed by De Nettancourt (2001). In common apricot and Japanese apricot, SI is determined by a single, multiallelic, S-locus, which contains two genes, the stylar S-RNAse gene and the pollen-expressed SFB/SLF (S-haplotype-specific F-box/S-locus F-box) gene (Entani et al. 2003; Romero et al. 2004; Ushijima et al. 2004; Zhang et al. 2008). Both genes exhibit the high polymorphism typical of plant SI loci, but the function of F-box is still unclear. Additional factors not linked to the *S*-locus could also be involved in the breakdown of SI in pollen-part mutants of apricots (Vilanova et al. 2006a). Inheritance of stylar S-RNAse was analyzed in common apricot by Burgos et al. (1998) and in Japanese apricot by Tao et al. (2002). Initially, cultivar genotyping was accomplished using a stylar ribonucleases analysis (Alburquerque et al. 2002). The development of PCR-based markers derived from both genes, S-RNAse and SFB, allowed the discrimination of three cultivar groups: SI group, one universal donor group and SC (self compatible group). This information was incorporated into breeding schemes for producing only self-compatible seedlings (Vilanova et al. 2005). Novel methods of S-allele screening (Vaughan et al. 2006) and dot-blot-*S*-genotyping (Kitashiba et al. 2008) were developed recently for large-scale S-haplotype detection and analysis.

7.4 Genomics

Structural genomics. Large-insert libraries and the physical genetic map developed for model peach genome are indispensable tools for map-based cloning of Mendelian loci in *Prunus*. However, some apricot specific genes such as those involved with self-incompatibility and PPV resistance could not be isolated from peach genomic libraries. To support apricot oriented projects, a BAC library derived from cultivar "Goldrich" was cloned into HindIII site of pBeloBAC11. The library containing

101,376 clones with an average insert size of 64 kb provides 22-fold apricot genome coverage (Vilanova et al. 2003a). The apricot genomic library facilitated a BAC-based cloning of the S-locus genes (Vilanova et al. 2005) and the saturation with SSRs markers in the upper portion G1 associated with PPV resistance (Vilanova et al. 2006b). Currently, this library is being used to sequence the PPV resistance region in 'Goldrich' genotype.

Functional genomics. Three sequenced cDNA libraries from different stages of fruit development (green, half-ripe and ripe mesocarp tissue) were sequenced, annotated and submitted to GeneBank (Grimplet et al. 2005). The total of 13,006 apricot ESTs represents transcriptional profiles of the apricot mesocarp tissue. They supported identification of gene transcripts differently expressed during fruit development in apricot (Geuna et al. 2005). In the *Prunus* database, EST collections from green and half-ripe apricots are the only source of genes expressed at early stages of mesocarp development in stone fruits. About 20% of the ESTs assembled into *Prunus* Unigene set_v 4 are of an apricot origin (Jung et al. 2008). So, apricot functional genomic resources were essential in the development of EST-SSRs and SNPs subsets available from GDR.

A proteomic study (a large-scale protein analysis) was applied for transcript profiling of F_1 individuals derived from crosses between SC and SI apricots. Qualitative and quantitative analyses of parental cultivars revealed 35 proteins with different expression patterns in SC and SI pistils and detected a posttranscriptional regulation of S-RNAse in SI apricots (Feng et al. 2006, 2007).

7.5 Transgenics

Genetic transformation allows discrete alteration of one or more traits in existing crop cultivars if an efficient tissue culture system is available. Transgenic apricot plants may be used as a tool to analyze individual traits through the identification of the corresponding genes and to study their regulation and expression. Understanding gene regulation at the cellular and whole plant level, and identifying and evaluating agriculturally useful genes, should also be possible.

Agrobacterium-mediated transformation of apricot. The virulence of the *Agrobacterium* strain varies with plant species (Cervera et al. 1998), and virulence can be stimulated by the presence of additional copies of the *virG* gene (Ghorbel et al. 2001). In apricots, variation in bacterial virulence between three wild-type *Agrobacterium* strains was not observed in greenhouse evaluation. However, differences in the number of Green Fluorescent Protein (GFP) spots per transformed explant were found when two disarmed strains were compared (Petri et al. 2004). Several environmental factors, including pH, temperature and osmotic stress, have been shown to affect *vir* gene expression (Alt-Mörbe et al. 1989). Stachel et al. (1985) reported that the addition of the phenolic compound acetosyringone (3′, 5′-dimethoxy-hydroxyacetophenone) to the culture medium also stimulated transcription of virulence genes in *Agrobacterium*.

Similar stimulatory effect of acetosyringone on bacterial virulence has been observed in apricot (Laimer da Câmara Machado et al. 1992; Petri et al. 2004). Apricot transformation can also be affected by the duration of cocultivation of inoculated explants with *Agrobacterium*. In general, the transformation frequency is increased with prolonged cocultivation, but a period longer than 3–4 days may cause problems of *Agrobacterium* overgrowth (Petri et al. 2004).

Selectable markers used for transformation. In apricot, GFP has been very useful to optimize early transformation steps. However, its expression is lost with increased plant development due to autofluorescence from chlorophyll, and can only be seen again in roots of developed transgenic shoots (Petri et al. 2008a, b).

Over-expression of regeneration-promoting genes may be a useful selection system as only transformed, but not nontransformed cells, can be regenerated into plants in the absence of growth regulators. The *ipt* gene from *Agrobacterium* (encoding isopentenyl transferase), a key enzyme of cytokinin biosynthesis, is a classical example of a regeneration-promoting gene. Constitutive expression of *ipt* can adversely affect plant growth and development. This can be prevented by placing the gene under the control of an inducible promoter (Kunkel et al. 1999) or in a MAT (multiautonomous transformation) vector, leading to its elimination from the transgenic plants (Ebinuma et al. 1997). Transformation of apricot with a MAT vector containing an *ipt* gene could notably improve the transformation efficiency (López-Noguera et al. 2009) compared to a standard transformation procedure (Petri et al. 2008a, b). Apart from *ipt*, information regarding other regeneration-promoting genes has been virtually lacking. Major efforts are being devoted to identify these genes, whose translation products may be associated with cytokinin synthesis and its recognition, or involved in promoting the vegetative-to-embryogenic or organogenic transition (Zuo et al. 2002).

Selection of transformed plants. Selection of transformed regenerants is a critical step in plant transformation. Antibiotics have been used most commonly as selection agents after integration of genes that confer antibiotic resistance. The concentration of the selective agent and timing of application must be optimized for each plant species. In apricot regeneration-inhibitory concentrations of the antibiotics kanamycin and paromomycin prevented regeneration of transformed plants and a progressive selection pressure with paromomycin, which has been shown to allow a better growth of transformed apricot tissues (Petri et al. 2005a), had to be used to recover transformed plants (Petri et al. 2006, 2008a).

Improvements in the genetic engineering of apricot. The regeneration of adventitious plants from seed-derived apricot tissues was first reported 20 years ago (Lane and Cossio 1986; Pieterse 1989; Goffreda et al. 1995). Using this approach the first apricot plants transformed with the gene encoding the coat protein (CP) of the plum pox virus (PPV) were obtained (Laimer da Câmara Machado et al. 1992). A similar approach was shown to be useful in plum (Ravelonandro et al. 1997), where a post-transcriptional gene silencing phenomenon was responsible for the acquired resistance in the transformed plums (Scorza et al. 2001) and it was shown to remain

stable under field conditions (Hily et al. 2004). Unfortunately, there is no further information available on the evaluation of the apricot plants transformed with the CP gene.

Transformation of seed-derived tissues for plants that are vegetatively propagated and with long generation cycles has a limited interest since agronomic characteristics of these plants are unknown and further breeding to introduce the transgene in commercially accepted cultivars needs many years of intensive work. Hence, much effort has been devoted to develop regeneration procedures from clonal tissues of commercial cultivars or new improved selections from breeding programs. The first report on adventitious regeneration from apricot leaves (Escalettes and Dosba 1993) found little reproducibility between experiments. A more effective and reproducible regeneration method from apricot leaves was established (Pérez-Tornero et al. 2000) and optimized latter, increasing regeneration percentages 200% by using ethylene inhibitors and specific gelling agents (Burgos and Alburquerque 2003).

Using the regeneration procedure developed for apricot leaves, an *Agrobacterium*-based transformation procedure was established for apricot leaves that yielded transgenic calluses, expressing *gfp* and *nptII* genes (Petri et al. 2004). The effect of aminoglycoside antibiotics for selection of apricot *nptII*-transformed leaf tissues was studied (Burgos and Alburquerque 2003; Petri et al. 2005a) and the transformation procedure optimized by adding 2,4-D during the cocultivation period (Petri et al. 2005b). However, transformed plants were not obtained.

Coupling transformation with different strategies to select transgenic cells and regenerate plants was necessary to obtain transformed plants. Regeneration inhibitory antibiotic concentrations applied after the coculture period did not allow regeneration of transformed plants and it was necessary to delay the selection pressure or reduce the antibiotic concentration during the first days after coculture before applying regeneration-inhibitory concentrations (Petri et al. 2008a). The first 14 days, including the coculture period, are a regeneration-induction period (in dark) and it is critical to obtain any regenerations from apricot leaves during this time (Pérez-Tornero et al. 2000). This key period probably allows dedifferentiation of leaf cells and differentiation again of those cells into meristems, which may explain the importance of the timing in the application of the selective agent.

Unfortunately, transformation procedures developed for apricot to date are very genotype-dependent, which does not allow using them as an efficient breeding tool.

Shortcomings in the transformation of apricot. Conventional breeding of apricot has been constrained by the long reproductive cycle of the species, with an extended juvenile growth phase, complex reproductive biology and high degree of heterozygosity. New technologies have the potential to reduce the time for cultivar development and offer alternative breeding strategies that are not available to breeders. Progress has been made for apricot in the areas of regeneration, *Agrobacterium*-mediated transformation, gene isolation and mapping, but several obstacles remain to be overcome. This is especially true for the development of a genotype-independent system for tissue culture and genetic transformation, which may be achieved by the

transformation of meristematic cells with a high regeneration potential and/or the use of regeneration-promoting genes (Petri and Burgos 2005). Also, the constraint should be addressed that European laws allow neither the deliberate release of plants carrying antibiotic resistance genes used in medicine or veterinary after 2004, nor their commercialization after 2008 (Directive 2001/18/EEC of the European Parliament and the Council of the European Union). The development of a selectable marker-free transformation system for apricot is therefore a priority in future studies.

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