

Chapter 14

Peach

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Abstract The peach is the third most produced temperate tree fruit species behind apple and pear. This diploid species, *Prunus persica*, is naturally self-pollinating unlike most of the other cultivated *Prunus* species. Its center of diversity is in China, where it was domesticated. Starting about 3,000 years ago, the peach was moved from China to all temperate and subtropical climates within the Asian continent and then, more than 2,000 years ago, spread to Persia (present day Iran) via the Silk Road and from there throughout Europe. From Europe it was taken by the Spanish and Portuguese explorers to the Americas. It has an extensive history of breeding

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that has resulted in scion cultivars with adaptability from cold temperate to tropical zones, a ripening season extending for 6–8 months, and a wide range of fruit and tree characteristics. Peach has also been crossed with species in the *Amygdalus* and *Prunophora* subgenera to produce interspecific rootstocks tolerant to soil and disease problems to which *P. persica* has limited or no resistance. It is the best known temperate fruit species from a genetics perspective and as a model plant has a large array of genomics tools that are beginning to have an impact on the development of new cultivars.

Keywords *Prunus persica* • History • Genetic resources • Breeding • Biotechnology • Interspecific • Hybrids • Model plant • Stone fruit • Drupe

1 Introduction

1.1 Economic Importance

The peach is the third most important temperate tree fruit species behind apples and pears. This total production is estimated at over 17.8 million tons. The production has more than doubled since 1980, from 7.7 to 17.8 million tons, mainly due to the rapid production increases seen in China. Production in the Americas and Europe has remained fairly steady with only small increases since 1980. Other countries that have more than doubled their production over the last 30 years are Korea, Chile, Spain, Egypt, Tunisia, and Algeria. The five largest producer countries are China, which accounts for ~46% of the world production, followed by Italy (~9%), Spain (~7%), the USA (~7%), and Greece (~4%) (USDA/ARS 2008; FAOSTAT 2010) (Table 14.1). Over 90% of this production is for the fresh market. Only nine countries (the USA, South Africa, Australia, Argentina, Chile, China, Spain, Greece, and Italy) are significant producers of processed peaches with the two largest producers, Greece and China, with an estimated production of 338,000 and 206,500 mt, respectively, in 2005 (FAS, USDA World and Export Opportunities 2006).

Table 14.1 World peach production (1,000 MT) from 1980 to 2008 (FAOSTAT, <http://www.fao.org> accessed 2 March 2010)

Region	1980–1984	1985–1989	1990–1994	1995–1999	2000–2004	2005–2008
World	7,679	8,335	10,434	11,758	14,746	17,840
Asia	1,433	1,832	3,062	4,657	7,179	10,106
Americas	2,060	2,033	2,248	2,244	2,509	2,407
Europe	3,827	4,115	4,637	4,048	4,208	4,319
Africa	261	282	408	710	725	867
Oceania	121	120	88	110	137	149

1.2 Uses

All the economically important cultivars belong to *Prunus persica* (L.) Batsch. The fruit may have melting, nonmelting, or stony hard flesh and varies in color from green to white to yellow and orange to red and purple, with various gradations and combinations of these tonalities. Peaches are mainly used as fresh fruit and processed to produce canned fruit, jellies, jams, juice, pulp for yogurts, and liquors. In some production regions, the seeds are utilized as rootstocks and the hard endocarp is used for charcoal production. The ornamental use of peach flowers is also significant, especially in China and Japan (Yulin 2002; Hu et al. 2005, 2006).

1.3 Taxonomy, Botany, and Basic Description of the Species

The peach belongs to the Rosaceae family, subfamily Prunoideae, genus *Prunus* (L.), subgenus *Amygdalus*, section *Euamygdalus*. Other subgenera besides *Amygdalus* within the genus *Prunus* are *Prunophora* (plums), *Cerasus* (cherries), *Padus*, and *Laurocerasus*. Commercial peach cultivars belong to the species *Prunus persica* (L.) Batsch. Related interfertile species include *P. dulcis* (Mill.) D. A. Webb, *P. davidiana* (Carr.) Franch, *P. ferganensis* (Kost and Rjab) Kov. & Kost, *P. kansuensis* Rehd, and *P. mira* Koehene. These species have primarily been used directly as or in the development of rootstocks and ornamentals but not in the development of scion cultivars. All originate from China with some range extension into Nepal and India (*P. mira*) and in the countries which previously formed the Soviet Union (*P. ferganensis*) (Scorza and Sherman 1996). *Prunus persica* can be hybridized with *P. dulcis*, *P. davidiana*, *P. ferganensis*, *P. kansuensis*, and *P. mira*, producing, in most cases, fertile hybrids (Watkins et al. 1995; Scorza and Okie 1990). Crosses between almond (*P. dulcis*) and peaches have been produced with several objectives, but mainly for rootstock development (Moreno 2004; Zarrouk et al. 2005; Felipe 2009; Pinochet 2009; Gradziel 2003; Martínez-Gómez and Gradziel 2002; Martínez-Gómez et al. 2004).

1.4 Distribution and Limits on Adaptation

Although the main production areas for the peach are located in both hemispheres between 30 and 45° latitude (Scorza and Sherman 1996), production is also found throughout the subtropics and tropical regions (Byrne et al. 2000). Disease and insect incidence is a limiting factor favored by conditions of high humidity. Windy, spring weather particularly favors the spread and infection by bacteria such as *Xanthomonas arboricola* (syn. *campestris*) pv. *pruni* ((Smith) Vauterin et al.), which

is one of the most important bacterial disease of peach in the world. High humidity and warm temperature can also favor the incidence of fungal diseases, such as brown rot (*Monilinia* spp.) and anthracnose (*Colletotrichum acutatum* Simmonds), whereas cooler conditions favor powdery mildew (*P. pannosa* (Wallr.: Fr.)) and peach leaf curl (*Taphrina deformans* (Berk.) Tul.).

Beyond the humidity related problems encountered throughout the latitudinal range of the peach, temperature related challenges are seen at the extreme latitudes at which peaches are grown. At high latitudes (45°N and S or above), minimum winter temperatures and spring frosts are the limiting factors. In those areas, flower bud death and consequently crop losses are not uncommon due to cold temperatures. The peach flower is bud hardy, depending on the cultivar, to about -25 to -30°C (Layne 1984). The northern range is extended where large bodies of water, such as the Great Lakes, and the Caspian and Black Seas, ameliorate the minimum temperatures. In latitudes lower than 20° such as Australia, Brazil, Thailand, and Taiwan, the lack of consistent chilling and high temperatures during bloom are important limitations. High temperatures during bloom increases the rate of pollen tube growth, stigma maturation and degeneration leading to poor fruit set (Burgos et al. 1991; Egea et al. 1991; Kozai et al. 2002). Highland tropical zones, which have cool and nonfreezing temperatures year round such as the cool highland mountains of Mexico, allow the possibility of manipulating flower induction, to have off-season harvest (Byrne 2010).

Thus, there is a great opportunity for breeders to improve cultivars especially for these marginal areas. However, even in the temperate zone, where adaptation may not be a problem, there is still much to improve, since market, climate, and consumer preferences change over the time.

2 Origin and Domestication

2.1 Origin and Evolution

The origin of peach in Asia and its domestication in China from where it was dispersed to Europe, Africa and America has been widely reported (Hedrick 1917; Hesse 1975; Westwood 1978; Scorza and Sherman 1996). However, little is known about the evolutionary history of the genus although homogamy studies suggest that the speciation of *P. persica* occurred from an allogamous (outcrossing) species such as *P. scoparia* (Spach) C.K. Schneider and *P. dulcis* (Weinbaum et al. 1986). It appears probable that *P. persica* and other species such as *P. dulcis*, *P. kansuensis*, *P. ferganensis*, *P. scoparia*, *P. mira*, and *P. davidiana* evolved from a common ancestor and are all closely related, as interspecific hybridization among them is common (Meader and Blake 1940; Knight 1969).

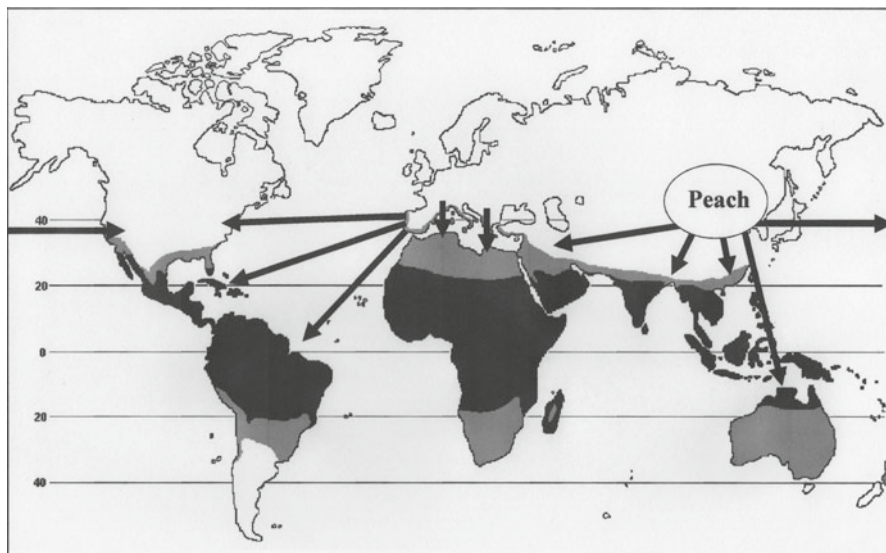


Fig. 14.1 Early dispersal of the peach. The peach dispersed throughout mainland Asia starting about 3,000 years ago and then to Japan and to Persia via the Silk road about 2,000 years ago. From there it was spread throughout Europe and northern Africa and eventually to the Americas by the Spanish and the Portuguese explorers in the sixteenth and seventeenth centuries. *White*, *gray*, and *black* areas are high chill, medium to low chill, and tropical zones, respectively. Modified from Byrne et al. 2000

2.2 Dispersal and Domestication

Starting about 3,000 years ago, the peach was moved from China to all temperate and subtropical climates within the Asian continent and about 1,500–2,000 years ago to Japan (Yamamoto et al. 2003). From Asia, the peach spread to Persia (present day Iran) via the Silk Road and from there throughout Europe more than 2,000 years ago. It was introduced to the Americas by the Spanish and Portuguese during the sixteenth century, where it was rapidly adopted by the Indians and spread to a wide range of environments (Hedrick 1917; Hesse 1975; Scorza and Okie 1990; Faust and Timon 1995), from the tropical highlands of South and Central America, to humid subtropics of Florida and southern Brazil and to the coldest regions in northern USA and southern Canada. There were probably several introductions from different parts of Spain, the Canary Islands, Portugal, and even from the South Pacific, since there were genotypes that adapted well to the humid subtropics (Fig. 14.1).

Seed propagation was the main source of plants up until the first half of the nineteenth century in the USA and Europe and to the middle of the last century in Central and South America. Thus, there are numerous landraces of peaches that have undergone several centuries of selection for adaptation and other characteristics throughout Europe, the Americas, Asia (Byrne et al. 2000; Bouhadida et al. 2007b, 2011; Pérez 1989; Pérez et al. 1993) and Japan (Yamamoto et al. 2003). Some of these traditional cultivars, propagated either by seed or budding, are still used today.

2.3 *Brief History of Peach Breeding*

In North America, it was only after the American Revolution in the 1770s when clonal propagation of peaches became a common technique (Hesse 1975). Several peach cultivars were released between the 1770s and the 1860s from selected seedlings of unknown parentage. About 1850, peaches were imported directly from China to North America, from which emerged the ‘Chinese Cling.’ This cultivar and its seedlings such as ‘Elberta,’ ‘Belle of Georgia,’ ‘J. H. Hale’ and their derivatives became important peach cultivars throughout the USA. This germplasm was central to the development of the fresh market cultivars in North America (Scorza et al. 1985; Faust and Timon 1995).

It was in the Americas, the region where the peach has been most recently introduced, where the first formal institutional breeding program was established. This was done in North America in 1895, in Geneva, New York. After this, programs were started in Iowa (1905), Illinois (1907), California (1907), Ontario (1911, Vineland and Harrow), New Jersey (1914), Virginia (1914), Massachusetts (1918), and New Hampshire (1918). A number of other states followed with Maryland and Michigan in the 1920s, Georgia and Texas in the 1930s, Louisiana, Florida, and North Carolina in the 1950s and Arkansas in the mid-1960s (Okie et al. 2008). Private breeding programs were established in California beginning in the 1930s (Okie et al. 2008; Faust and Timon 1995). Most of these programs emphasized the development of locally adapted peaches and nectarines with melting flesh for the fresh market. In Latin America, breeding programs were initiated in southern Brazil at two locations (Pelotas and Sao Paulo) to develop both nonmelting and melting flesh cultivars for both the fresh and processing outlets in the 1950s and in Mexico to develop their nonmelting peaches for the fresh market in the 1980s (Byrne et al. 2000; Byrne and Raseira 2006). Other smaller efforts in developing well adapted peach cultivars are ongoing in Chile, Uruguay, and Argentina.

In Europe, even though peach culture was widespread back in the Middle Ages in France, the first peach breeding program was begun in Italy in the 1920s and later in the 1960s in France. Subsequently, additional programs were established in Spain, Romania, Serbia, Greece, Bulgaria, Ukraine, and Poland (Okie et al. 2008; Llácer 2009). Much of the initial work was based on the cultivars developed in the USA so many of the European cultivars are closely related to North American cultivars (Faust and Timon 1995). These programs include both privately and publically funded programs.

In Asia, where peaches have been cultivated for several thousands of years, the earliest formal breeding program was started 50–60 years ago in Japan followed by multiple breeding efforts in China (1970s) and most recently in Korea, India, and Thailand (Byrne et al. 2000; Okie et al. 2008; Raseira et al. 2008). It is interesting to note that ‘Shanghai Suimitsuto’ (=‘Chinese Cling’) has also played a key role in the breeding of Japanese cultivars as was seen with North American cultivars (Ma et al. 2006; Xu et al. 2006; Yamamoto et al. 2003).

In South Africa and Australia, the emphasis has historically been on nonmelting flesh peaches. Subsequently, these efforts have expanded to fresh market peaches in both melting and nonmelting flesh (Byrne et al. 2000; Topp et al. 2008).

As the programs evolved, the basic objectives such as productivity, size, excellent appearance, season extension, and firmness are uniform throughout the programs. The major change has been in an increased emphasis in fruit quality, postharvest life, disease and pest resistance, a greater diversity of fruit types, and adaptation to low-chill zones (Byrne 2005). The most dramatic change in peach breeding programs, however, has been the reduction of public breeding and an increase in the private sector breeding programs, which now release the majority of the peaches and nectarines in the USA, France, and Spain. In the USA, about 50% of the public stone fruit breeding programs have closed since 1970. Most of the remaining public breeding programs release new cultivars with patent protection to generate funding for their programs. Even if this is currently a viable approach, in the long term it can create problems by limiting fundamental research in genetics and germplasm resources as well as germplasm exchange among programs (Byrne 2005; Okie et al. 2008). This lack of germplasm exchange is partially counterweighed by the fact that the UE legislation allows the free use of pollen from patented cultivars.

3 Genetic Resources

3.1 *Geographic Germplasm Groups*

Early domesticates used for fruit were most likely seedlings and coexisted with wild peach seedlings in several geographic regions in China (Wang 1985; Scorza and Okie 1990; Faust and Timon 1995). In China, there are several regional groups of fruiting cultivars: the northern and northwest group, the southern group, and the low-chill group (Yoon et al. 2006; Anderson 2009). The northern and northwestern group includes genotypes adapted to cold winters and hot dry summers and includes the Miantao and Mintao white peach groups, which are drought and cold tolerant, as well as yellow flesh peaches and a few nectarines. The southern group is adapted to a humid subtropical to temperate climate and relatively mild winters. These are generally white, subacid and include many pantao cultivars. It is represented by the ‘Shanghai Shuimi’ and ‘Chinese Cling’ peaches which were central in the development of the cultivated peaches developed in Japan (Yamamoto et al. 2003), the USA, and Europe (Scorza et al. 1985; Byrne et al. 2000; Aranzana et al. 2003a). The low-chill group, represented by landraces from Taiwan, Thailand, and southern China, is generally small fruited peaches of low quality. Several of these (‘Okinawa’ and ‘Hawaiian’) served as a source of the low-chill trait in the development of the low-chill germplasm in the Florida and Texas breeding programs (Byrne and Bacon 1999; Byrne et al. 2000).

As peaches were moved throughout the world and seed propagated, a series of landraces were developed outside of China that were adapted to a diverse range of climates and selected for regional quality preferences. It appears that many of these landraces and consequently commercial cultivars outside China are derived from the Southern China geographic group as indicated by inbreeding analyses (Scorza et al.

1985, 1988; Byrne and Bacon 1999; Byrne 2003; Byrne and Raseira 2006) and studies with molecular markers (Warburton and Bliss 1996; Yoon et al. 2006; Anderson 2009). Nevertheless, within these groups there are clustering of the genotypes by regional groups (Anderson 2009; Marchese et al. 2005; Badenes et al. 1998; Bouhadida et al. 2007a, b, 2011) and breeding history (Anderson 2009; Yoon et al. 2006; Warburton and Bliss 1996; Aranzana et al. 2003a; Bouhadida et al. 2011). In general, the highest genetic diversity seen was among the northern and northwestern and the low-chill groups and the least among the highly bred cultivars from the USA and Europe (Anderson 2009; Yoon et al. 2006; Warburton and Bliss 1996; Chen et al. 2007).

3.2 *Related Species in Breeding*

Prunus persica is interfertile with its related species *P. dulcis*, *P. kansuensis*, *P. ferganensis*, *P. scoparia*, *P. mira*, and *P. davidiana*, and interspecific hybridization among them is common (Meader and Blake 1940; Knight 1969). Nevertheless, scion cultivars are almost exclusively developed from *Prunus persica* although there is some work with some interspecifics especially within the *Amygdalus* section as a source of PPV, powdery mildew, and aphid resistance and for several growth and adaptation traits in scion breeding (Gradziel 2003; Martínez-Gómez et al. 2004; Byrne et al. 2000; Foulongne et al. 2003a, b). The major reason for this is that once the interspecific cross is made it takes from three to five generations to recover the necessary commercial fruiting traits. This is not necessary for the development of ornamental cultivars (Hu et al. 2006) and rootstocks, and thus, a wider range of species have been used.

The most common rootstocks are those derived from species within the section *Euamygdalus* Schneid including peach seedlings (*P. persica*), closely related species to peach (*P. dulcis*, *P. davidiana*, *P. ferganensis*, *P. kansuensis*, and *P. mira*) and interspecific hybrids of peach \times almond and peach \times *P. davidiana*. Peach is generally graft-compatible with itself and most species within its taxonomic Section *Euamygdalus* (Zarrouk et al. 2006). Peach seedlings have been the main rootstock source for peach on a worldwide basis. Seeds from wild types, commercial cultivars (from canning industry) and special rootstock selections are easily obtained and multiplied in the nursery. In China, seeds of *P. davidiana*, *P. ferganensis*, *P. kansuensis*, and *P. mira* have been also used as rootstocks (Wang et al. 2002; Yulin 2002). The peach \times almond hybrids are primarily used in calcareous soils, since they tolerate iron chlorosis well and are graft compatible with peach. They are also vigorous and therefore, appropriate for use in poor, dry soils and in fruit tree replanting situations (Bernhard and Grasselly 1981; Kester and Assay 1986; Egilla and Byrne 1989; Moreno et al. 1994; Felipe 2009). The peach \times *P. davidiana* hybrids induce in general good productivity to peach scions, and their selections are resistant to root-knot nematodes (Edin and Garcin 1994).

Although graft compatibility can be an issue, rootstocks from various *Euprunus* species have also been employed as peach rootstocks (Layne 1987; Reighard and

Loreti 2008). This group includes the hexaploid plums (European plums—*P. domestica* L., or St. Julien and ‘Pollizo de Murcia’ plums—*P. insititia* L.) because the graft compatibility with peaches is generally good. It also includes the diploid (Myrobalan or cherry plum—*P. cerasifera* Ehrh. and Japanese plums—*P. salicina* Lindl.) and tetraploid plums (Sloe—*P. spinosa* L.). In addition, there are numerous interspecific hybrids with different ploidy levels such as the Marianna plums (*P. cerasifera* × *P. munsoniana* W. Wight & U.P. Hedrick). Peach compatibility on fast-growing plums (*P. cerasifera* and interspecific hybrids with this species) differs substantially depending on the evaluated genotype (Zarrouk et al. 2006) and typical “translocated” incompatibility symptoms are frequently seen (Moreno et al. 1993). In the case of ‘Damas GF 1869’ (a pentaploid rootstock, probably *P. domestica* × *P. spinosa*), at least two dominant alleles are responsible for the incompatibility (Salesses and Alkai 1985), but another type of genetic control might be involved in the case of Myrobalan (Salesses and Bonnet 1992; Pina and Errea 2005). Excessive suckering may occur with several plum rootstocks, mainly if they are micropropagated.

Plum rootstocks are more tolerant to compact soils and waterlogging than other species of *Prunus* L., a fundamental reason for their use (Rowe and Catlin 1971; Salesses and Juste 1970; Xiloyannis et al. 2007). In addition, some of them provide greater tolerance to fungal diseases (*Phytophthora* crown rot, *Armillaria* root rot) favored by waterlogged and/or replant problems in the soil. A more stable resistance to root-knot nematodes (*Meloidogyne* species) can also be found in plum, when compared with resistant peach and almond sources that express a near-complete or incomplete spectrum of resistance (Pinochet et al. 1999; Dirlewanger et al. 2004a, c). Moreover, some Myrobalans are highly resistant or immune to all root-knot nematode species, even under high and continuous inoculum pressure and high temperatures (Esmenjaud et al. 1996). This resistance is attributed to three major genes, *Ma1*, *Ma2*, and *Ma3* (Lecouls et al. 1997; Rubio-Cabetas et al. 1998).

More recently, especially because of improved propagation techniques, there has been the development of interspecific hybrids between species from Sections *Euamygdalus* and *Euprunus*, and rootstocks or hybrids from Sections *Prunocerasus* Koehne and *Microcerasus* Webb. In spite of the sterility these interspecific hybrids have been made with the purpose of bringing together the desirable traits of plum, almond, and peach species (Hesse 1975; Scorza and Okie 1990; Pérez and Moore 1985; Moreno 2004). Once the hybrids are created, they are selected for their ease of propagation as well as the adaptation traits of interest.

3.3 Germplasm Collections

The most extensive collections of peach germplasm have been assembled in China. Since the 1960s most of China has been explored and collections made of the peach germplasm including several of the related species. Thus, these collections include many of the local cultivars and landraces from China where this crop was domesticated

as well as introduced cultivars from throughout the world. In the 1980s, China established three national peach repositories in Nanjing, Zhengzhou, and Beijing. The collection in Nanjing has 560 accessions and is focused on the southern germplasm and resistance to various diseases and waterlogging. The Beijing collection (280 accessions) houses the northern peach germplasm and the Zhengzhou repository (650 accessions) focuses on the germplasm collected from the northwest of China including accessions from the five related species (Wang and Zhang 2001; Wang et al. 2002). Other significant national collections would be those in Japan (600 accessions), Korea (300 accessions), the USA (280 accessions including four related species and an almond germplasm collection of about 100 accessions), Brazil (732), Ukraine (~1,500 accessions), and over 2,000 accessions in Europe with the largest collections in France, Spain (Bouhadida et al. 2011) and Italy. Beyond the collections in China, these collections tend to consist primarily of commercial cultivars with some accessions to represent wild seedlings, rootstocks, traditional cultivars, and landraces.

4 Major Breeding Achievements

4.1 Scion Cultivars

There are hundreds of peach and nectarine cultivars used commercially throughout the world (Ctifl 1994; Brooks and Olmo 1997; Okie 1998; Yulin 2002). In fact, the international peach breeding community has been very active and over the past several decades have released about 100 new cultivars per year (Della Strada and Fideghelli 2003; Fideghelli et al. 1998). The three most important achievements in peach breeding have been the expansion of its adaptation, the extension of its harvest period, and the diversification of its market.

The first step in this expansion of its adaptation was the dispersal of the peach via seed from its origin in north and northwest China to southern China and then throughout the world. During this early dispersal, the peach was selected for local adaptation from tropical to high latitude temperate zones over a period of centuries. Once breeding programs were initiated this raw germplasm was used to develop better commercial cultivars. Currently, the most active of this breeding is the development of early ripening medium and low-chill peach and nectarine cultivars mainly driven by the desire to have fruit available year round. Beyond, adaptation to temperature variations, work has resulted in peach cultivars resistant to bacterial leaf and fruit spot (*Xanthomonas arboricola* pv. *pruni* (Smith) Vauterin et al.). Unfortunately little work has been done on other major diseases such as brown rot, powdery mildew, peach scab, rust, anthracnose among others because they were either only regionally important, caused occasional damage, or could be easily controlled by chemical applications. Currently, given more restrictions on chemical use, approaches to minimize the use of chemicals via cultural control and

the development of disease resistance are being emphasized (Byrne et al. 2000; Byrne 2005).

The extension of the harvest season has been the objective of countless breeding programs and has resulted in expanding a 1- to 2-month harvest season to one that can be as long as 8 months. Much of this was done by manipulating the fruit development period but this was also supplemented by selecting for earlier blooming genotypes. Thus, in regions where spring frosts are not a production limitation, the earliest ripening genotypes are also the earliest blooming. Beyond this, cultivars were also selected for adaptation to lower chill zones where the bloom occurred earlier and thus had the potential of earlier ripening as well.

Finally, the market for peaches has been expanded to two ways. First, the locally marketed peach of the 1900s was transformed into a peach suitable for national and international markets by significantly improving fruit size, appearance and firmness. Unfortunately, the progress in raising the internal qualities such as sugar and antioxidants content, tolerance to internal breakdown (IB) and other postharvest traits has lagged behind, but recently there has been an increased emphasis on these factors in several breeding efforts (Byrne 2005; Peace et al. 2006; Cantín et al. 2009a, b, 2010b). The other strategy for increasing its market share has been the development of new products. The best example of this would be the development of the nectarine as another fruit. This process began in the 1950s in the USA and now nectarine production is about 40% of the fresh peach production. This diversification of the fresh peach products available continues today (Byrne 2005).

4.2 Rootstocks

The range of rootstocks now available for peach worldwide has increased dramatically in the last few decades (Table 14.2). With the improvement of vegetative propagation technology for *Prunus*, including tissue culture, many of the breeding programs have focussed on the generation of complex *Prunus* species hybrids to overcome soil and disease problems to which *P. persica* has limited or no resistance (Reighard 2002; Moreno 2004; Reighard and Loreti 2008).

Considerable progress has been made in developing iron chlorosis tolerant rootstocks, using peach × almond hybrids, first from open pollinated or wild germplasm sources, and in the last two decades with controlled interspecific hybridization. Research on peach–almond hybrid rootstocks tolerant to iron-chlorosis, ease of vegetative propagation and graft compatibility with peach led to the selection of highly vigorous rootstocks such as ‘GF 677’ (Bernhard and Grasselly 1981), which have been widely adopted in the Mediterranean basin countries. Other regional selections are ‘Adafuel’ (Cambra 1990; Moreno et al. 1994), ‘Mayor’ (Cos et al. 2004) and ‘Sirio’ (Loreti and Massai 1994). Unfortunately all of these are susceptible to root-knot nematodes. Recently, three high-vigor peach–almond hybrids (e.g., ‘Monegro,’ ‘Garnem,’ and ‘Felinem’) have been derived from a cross between the almond

Table 14.2 List and description of commercial or released peach rootstocks

Rootstock ^a	Species	Origin	Calcareous soil tolerance	Waterlogging tolerance	Root-knot nematodes resistance	Other characteristics	References
<i>Peach-based rootstocks (Section Eucamydalus)</i>							
GF 305	<i>P. persica</i>	INRA, France	Susceptible	Susceptible	Susceptible (Ma, Mi) Resistant (Mj, Mh)	Easy propagation	Grassely (1983); Salesses et al. (1970); Esmerijaud et al. (1994)
Guardian™	<i>P. persica</i>	USDA-ARS and Clemson U., The USA	Susceptible	Susceptible	Resistant (Mi, Mj)	Tolerant to PTSL, bacterial canker complex	Beckman et al. (1997); Nyczepir et al. (2006); Reighard and Loreti (2008)
Lovell, Halford	<i>P. persica</i>	UC, The USA	Susceptible	Susceptible	Susceptible	Easy propagation	Egilla and Byrne (1989); Lu et al. (2000); Reighard and Loreti (2008)
Missour	<i>P. persica</i>	Unknown, Morocco	Susceptible	Susceptible	Unknown	Easy propagation	Tagliavini and Rombola (2001)
Montclair	<i>P. persica</i>	INRA, France	Moderately tolerant?	Moderately tolerant	Susceptible	Easy propagation	Grassely (1988); Fernández et al. (1994); Shi and Byrne (1995)
P.S.B2	<i>P. persica</i>	U Pisa, Italy	Susceptible	Susceptible	Resistant	Yield efficiency	Loreti and Massai (2006); Reighard and Loreti (2008)
Rubira	<i>P. persica</i>	INRA, France	Susceptible	Moderately tolerant	Susceptible	Red leaf	Grassely (1988); De Salvador et al. (2002)
Siberian C	<i>P. persica</i>	ACRS, Canada	Susceptible	Susceptible	Susceptible	Cold hardiness	Layne (1987); Reighard and Loreti (2008)
Barrier 1	<i>P. persica</i> x <i>P. davidiana</i>	CNR, Italy	Moderately tolerant	Moderately tolerant	Resistant	High vigor	De Salvador et al. (1991, 2002)
Cadaman™	<i>P. persica</i> x <i>P. davidiana</i>	France-Hungary	Moderately tolerant	Moderately tolerant	Resistant (Mj)	Yield efficiency, high vigor	Edin and Garcin (1994); Pinochet et al. (1999); Zarrouk et al. (2005)

Flordaguard	<i>P. persica</i> × <i>P. davidiana</i>	U. Florida, The USA	Highly susceptible	Susceptible	Resistant (Mj, Mi)	Red leaf, high vigor	Pinochet et al. (2002)
Nemaguard	<i>P. persica</i> × <i>P. davidiana</i>	USDA-ARS, The USA	Highly susceptible	Susceptible	Resistant (Ma, Mi, Mj)	Easy propaga- tion, high vigor	Layne (1987); Shi and Byrne (1995)
Nemared	(<i>P. persica</i> × <i>P. davidiana</i>) × <i>P. persica</i>	USDA-ARS, The USA	Highly susceptible	Susceptible	Resistant (Ma, Mi, Mj)	Red leaf, easy propagation	Ramming and Tanner (1983); Marull et al. (1994); Lu et al. (2000)
Adafuel ^{PVP}	<i>P. dulcis</i> × <i>P. persica</i>	CSIC, Spain	Highly tolerant	Susceptible	Susceptible (Mj)	High vigor, easy propagation	Cambra (1990); Moreno et al. (1994); Albás et al. (2004); Zarrouk et al. (2005)
Adarcias ^{PVP}	<i>P. dulcis</i> × <i>P. persica</i>	CSIC, Spain	Tolerant	Moderately tolerant	Susceptible	Control of tree vigor, higher fruit quality	Moreno et al. (1994); Zarrouk et al. (2005); Albás et al. (2004)
Felinem ^{PVP}	<i>P. dulcis</i> × <i>P. persica</i>	CITA, Spain	Highly tolerant	Susceptible	Resistant (Ma, Mi, Mj, Mhi)	Red leaf, high vigor	Felipe (2009); Dichio et al. (2004); Zarrouk et al. (2005)
Garnem ^{PVP}	<i>P. dulcis</i> × <i>P. persica</i>	CITA, Spain	Tolerant	Susceptible	Resistant (Ma, Mi, Mj, Mhi)	Red leaf, high vigor	Felipe (2009); Pinochet et al. (1999); Marull et al. (1994); Dichio et al. (2004); Zarrouk et al. (2005)
Monegro ^{PVP}	<i>P. dulcis</i> × <i>P. persica</i>	CITA, Spain	Highly tolerant	Susceptible	Resistant (Ma, Mi, Mj, Mhi)	Red leaf, high vigor	Felipe (2009)
GF 677	<i>P. dulcis</i> × <i>P. persica</i>	INRA, France	Highly tolerant	Susceptible	Susceptible (Ma, Mi, Mj, Mh)	High vigor, easy propagation	Bernhard and Grasselly (1981); Salesses et al. (1970); Dichio et al. (2004); Zarrouk et al. (2005); Jiménez et al. (2008)

(continued)

Table 14.2 (continued)

Rootstock ^a	Species	Origin	Calcareous soil tolerance	Waterlogging tolerance	Root-knot nematodes resistance	Other characteristics	References
GF 557	<i>P. dulcis</i> × <i>P. persica</i>	INRA, France	Highly tolerant	Susceptible	Resistant (Mi) Susceptible (Mj)	High vigor	Bernhard and Grasselly (1981); Saleuses et al. (1970); Esmenjaud et al. (1994)
Castore, Polluce	<i>P. dulcis</i> × <i>P. persica</i>	U Pisa, Italy	Tolerant	Susceptible	Unknown	Control of vigor, high fruit quality	Loreti and Massai (2006); Reighard and Loreti (2008)
Sirio	<i>P. dulcis</i> × <i>P. persica</i>	U Pisa, Italy	Tolerant	Susceptible	Susceptible (Mj)	Control of vigor	Loreti and Massai (1994); Pinochet et al. (1999)
Hansen 536	<i>P. dulcis</i> × <i>P. persica</i>	UC, The USA	Tolerant	Susceptible	Resistant (Ma, Mi, Mj)	High vigor	Kester and Assay (1986); Felipe et al. (1997b)
Hansen 2168	<i>P. dulcis</i> × <i>P. persica</i>	UC, The USA	Tolerant	Susceptible	Resistant (Ma, Mi)	High vigor	Kester and Assay (1986); Felipe et al. (1997b)
Nickels	<i>P. dulcis</i> × <i>P. persica</i>	UC, The USA	Tolerant	Susceptible	Resistant	High vigor	Reighard and Loreti (2008)
<i>Plum-based rootstocks (Section Euprumus)</i>							
Adesoto 101 ^{PVP}	<i>P. insititia</i>	CSIC, Spain	Highly tolerant	Highly tolerant	Immune (Ma, Mi, Mj)	Yield efficiency	Moreno et al. (1995); Pinochet et al. (1999); Jiménez et al. (2008)
Montizo™	<i>P. insititia</i>	CITA, Spain	Tolerant	Tolerant	Resistant (Ma, Mi, Mj)	Yield efficiency	Felipe et al. (1997a)
Monpol™	<i>P. insititia</i>	CITA, Spain	Tolerant	Tolerant	Resistant	Medium vigor	Felipe et al. (1997a)
St. Julien A	<i>P. insititia</i>	East Malling, UK	Moderately tolerant	Tolerant	Unknown	Medium to low vigor	Okie (1987)
GF 655/2	<i>P. insititia</i>	INRA, France	Moderately tolerant	Susceptible	Resistant (Ma, Mi, Mj)	Excessive suckering	Grasselly (1988); Saleuses et al. (1970); Layne (1987)

Brompton	<i>P. domestica</i>	East Malling, UK	Moderately tolerant	Moderately tolerant	Resistant (Ma, Mi, Mj)	Medium vigor	Salleses et al. (1970); Layne (1987); Okie (1987)
Penta	<i>P. domestica</i>	CRA-FRU, Italy	Tolerant	Tolerant	Resistant (Mj)	Medium vigor	Nicotra and Moser (1997); Pinochet et al. (2002)
Tetra	<i>P. domestica</i>	CRA-FRU, Italy	Tolerant	Tolerant	Resistant (Mj)	Medium vigor	Nicotra and Moser (1997); Pinochet et al. (1999)
Damas GF 1869	<i>P. domestica</i> × <i>P. spinosa</i>	INRA, France	Highly tolerant	Highly tolerant	Resistant (Mi)	Excessive suckering and graft incompatibility	Grasselly (1988); Zarrouk et al. (2006)
Mr.S.2/5 Jasp1™	<i>P. cerasifera</i> <i>P. salicina</i> × <i>P. spinosa</i>	U Pisa, Italy INRA, France	Tolerant Tolerant	Tolerant Tolerant	Resistant (Mi, Mj) Resistant	Medium vigor Peach compatibility?	Reighard and Loreti (2008) Bernhard and Renaud (1990); De Salvador et al. (2002)
<i>Rootstocks based on hybrids among sections Eucamysdatus, Euprunus, Prunocerasus, and Microcerasus</i>							
Controller 5™	<i>P. salicina</i> × <i>P. persica</i>	UC, The USA	Susceptible	Susceptible	Susceptible	Control of peach vigor	DeJong et al. (2004); Reighard and Loreti (2008)
Ishtara™	(<i>P. cerasifera</i> × <i>P. salicina</i>) × (<i>P. cerasifera</i> × <i>P. persica</i>)	INRA, France	Susceptible	Moderately tolerant	Immune (Mj)	Tolerance to <i>Armillaria?</i> Highly susceptible to bacterial canker	Grasselly (1988); Renaud et al. (1988); Guillaumin et al. (1991); Pinochet et al. (1999)
Hiawatha	<i>P. besseyi</i> × <i>P. salicina</i>	Unknown, Canada	Susceptible?	Unknown	Resistant (Mj)	Peach graft compatibility?	Pinochet et al. (2002)
Evrica	(<i>P. besseyi</i> × <i>P. salicina</i>) × <i>P. cerasifera</i>	KEBS, Russia	Susceptible	Moderately tolerant	Resistant (Mj)	Peach graft incompatibility	Zarrouk et al. (2006)

(continued)

Table 14.2 (continued)

Rootstock ^a	Species	Origin	Calcareous soil tolerance	Waterlogging tolerance	Root-knot nematodes resistance	Other characteristics	References
Bruce	<i>P. salicina</i> × <i>P. angustifolia</i>	Texas A&M, The USA	Unknown	Unknown	Immune (Mj)	Peach graft incompatibility	Pinochet et al. (1999, 2002); Zarrouk et al. (2006)
Pumiselect	<i>P. pumila</i>	Geissenheim, Germany	Susceptible	Susceptible	Resistant (Mj)	Cold hardiness, Scion dwarfing	Jacob (1992); Reighard and Loreti (2008); Pinochet et al. (2002)
Krymsk-86™	<i>P. cerasifera</i> × <i>P. persica</i>	KEBS, Russia	Tolerant	Moderately tolerant	Susceptible (Mj)	Cold hardiness, tolerance to Pv	Jiménez et al. (2008); Reighard and Loreti (2008)

Root-knot nematodes (*Meloidogyne* spp.): Ma: *M. arenaria*; Mi: *M. incognita*; Mj: *M. javanica*; Mh: *M. hapla*; Mhi: *M. hispanica*. Lesion nematodes (*Pratylenchus vulnus*): Pv

ACRS Agriculture Canada Research Station at Harrow (Canada), CITA Centro de Investigación y Tecnología Agroalimentaria de Aragón (Spain), CNR Centro Nazionale della Ricerca Consiglio Nazionale delle Ricerche (Italy), CSIC Consejo Superior de Investigaciones Científicas (Spain), GB Gregory Brothers, California (The USA), Geissenheim Geissenheim Research Station (Germany), INRA Institut National de la Recherche Agronomique (France), CRA-FRU Centro di Ricerca per la Frutticoltura (Italy), UC University of California (USA), USDA-ARS US Department of Agricultural Research Service (The USA), U Pisa University of Pisa (Italy), Texas A&M University of Texas, College Station (The USA), KEBS Krymsk Experimental Breeding Station (Russia), PVP Plant Variety Protection by Community Plant Variety Office in the European Union

^aNext the Rootstock

'Garfi' × 'Nemared' peach that are resistant to root-knot nematodes and tolerant to calcareous soils have been released (Felipe et al. 1997b; Felipe 2009). These rootstocks have red leaves, a desirable nursery character in rootstocks because of the ease with which failed grafts can be discarded. Other peach–almond and peach × *P. davidiana* hybrids resistant to root-knot nematodes are 'Barrier 1,' 'Cadaman' (Edin and Garcin 1994), 'Hansen 536,' and 'Hansen 2168' (Kester and Assay 1986), but these are less tolerant to iron-chlorosis than 'GF 677' (Jiménez et al. 2008).

Other advances have been made in developing waterlogging and compact soil tolerant plum based rootstocks that are graft compatible with peach. Furthermore, some are tolerant to iron-induced chlorosis, are more precocious, and produce fruits of higher quality (Moreno et al. 1995; Felipe et al. 1997a; Nicotra and Moser 1997). Rootstocks tolerant to waterlogged soils include 'Adesoto 101,' 'Jaspi,' 'Julior,' 'Montizo,' 'Mr.S. 2/5,' 'Penta,' 'Tetra,' and 'Krymsk 86' (Table 14.2). The Tsukuba series of rootstocks from Japan and several peach × *P. davidiana* hybrids have been reported to show some tolerance to waterlogging (Reighard 2002; Zarrouk et al. 2005; Xiloyannis et al. 2007).

There are extensive efforts in Europe and in the USA to obtain resistance to root-knot nematodes (*Meloidogyne* spp.), which cause serious growth reduction in peach trees grown in warmer regions. There are at least five species of root-knot nematodes (*M. arenaria*, *M. incognita*, *M. javanica*, *M. hapla*, and *M. floridensis*) as well as a number of races within each species that feed on peach. Acceptable resistance for the predominant species has been incorporated into rootstock cultivars in different programs from several countries (Fernández et al. 1994; Pinochet 2009; Pinochet et al. 1999; Moreno 2004; Reighard and Loreti 2008: the USA ('Nemaguard,' 'Nemared,' 'Flordaguard,' 'Guardian®,' 'Hansen 536,' and 'Hansen 2168'), Spain ('Adesoto 101,' 'Adara,' 'Monegro,' 'Garnem,' 'Felinem,' and 'Greenpac'), France ('Myran,' 'Ishtara,' 'Cadaman,' and 'Julior'), Germany ('PumiSelect'), Italy ('Barrier 1,' 'Penta,' and 'Tetra'), Japan ('Juseitou' and 'Okinawa'), and China ('Gansutao 1' and 'Shouxingtao 1').

Considerable efforts have been undertaken to find a resistant or tolerant rootstock for peach in areas where peach tree short life (PTSL) syndrome is limiting tree longevity in the southeastern USA. In South Carolina and Georgia, a rootstock with acceptable survival in field tests has been developed and released under the name Guardian™ (Okie et al. 1994; Reighard et al. 1997).

Recently, an increased emphasis has been placed on developing dwarfing or semidwarfing rootstocks adapted to different soil fertilities and allowing higher density in the orchard. Several promising size-controlling clonal rootstocks have been released. These include the peach–almond hybrids 'Adarcias' (Moreno et al. 1994), 'Castore,' 'Polluce,' and 'Sirio' (Loreti and Massai 1994; 2006); the *P. salicina* × peach hybrid 'Controller 5' (DeJong et al. 2004); the complex plum–peach hybrid 'Ishtara' (Renaud et al. 1988), and the plum rootstocks 'Adesoto 101,' 'Montizo,' 'Penta,' and 'Tetra' (Moreno et al. 1995; Felipe et al. 1997a; Nicotra and Moser 1997).

5 Current Goals and Challenges of Breeding

5.1 *Scion Cultivars*

The ultimate goal of the breeder is to develop cultivars that have superior and consistent fruit production, quality and market appeal. This involves combining a range of adaptation, tree growth/fruiting, and fruit traits into one cultivar that will satisfy the producer, the packer, the merchandiser, and ultimately the consumer. Production consistency relies on excellent adaptation to the regions especially with respect to the yearly variations in temperature and humidity. Major objectives for adaptive traits include cold hardiness, chilling requirement and bloom time, and the tolerance to high heat during bloom in the lower chill zones. In the more humid regions, there is an increasing pressure to reduce the use of crop protectants, and consequently many of these programs breed for resistance to the common diseases such as brown rot, bacterial leaf and fruit rot, powdery mildew, peach leaf curl, and the plum pox virus (PPV).

Given that high tree productivity has been obtained in new cultivars, the next goal would be a tree architecture that is easy to manage but remains very productive. Labor is a major limiting input for fruit production in many production areas and consequently there has been substantial work in developing specific growth types such as pillar and weeping forms as well as in developing growth controlling rootstocks that will contribute to better designed and/or smaller trees that require less pruning, less time to manage and are more efficient producers of quality fruits (Byrne 2005; Sansavini et al. 2006).

The peach fruit can have a range of colors, textures and rate of softening, shapes, sizes, and flavors. Furthermore, what is preferred by the consumer changes with region although there is a trend to make a greater range of fruit types available in any given market. This diversification of the fruit types available will continue as many breeding programs are working toward this objective (Byrne 2005; Sansavini et al. 2006). Specific objectives include orange and red flesh colors, the lack of anthocyanins, higher sugar content, and better health promoting properties such as high levels of antioxidant phytochemicals (Vizzotto et al. 2007; Cantín et al. 2009a, b).

Another increasingly important objective is the improved postharvest behavior of the fruit. This has been a focus of breeding in regions such as Chile and South Africa where the fruit is routinely exported and is becoming increasingly important in other major production areas especially in breeding programs which are global in scope (Infante et al. 2008; Byrne 2005; Okie et al. 2008; Cantín et al. 2010b). The major impediment is the cost of evaluating selections for major postharvest traits such as the resistance to IB and specific flesh types, though good progress is being made to find molecular markers for these traits (Iezzoni et al. 2009; Ogundiwin et al. 2009; Cantín et al. 2010b; Peace et al. 2005, 2007).

5.2 Rootstocks

In the Mediterranean countries, where the European peach industry is primarily located, a new generation of peach rootstocks is being developed with the collaboration of different groups from France, Italy, and Spain. The objectives are to obtain genotypes with greater resistance to abiotic (iron chlorosis, waterlogging, and drought) and biotic stresses (*Meloidogyne* spp. nematodes, *Phytophthora* and *Armillaria* fungal diseases, replant disorders), and to improve peach graft compatibility and control of scion vigor (Salesses et al. 1998; Dirlewanger et al. 2004c; Moreno 2004; Pinochet et al. 2005). Controlled interspecific crosses have been undertaken with the purpose of bringing together the desirable traits of different *Prunus* species. Thus, some Myrobalan genotypes were chosen as parents for their high level and wide spectrum of root-knot nematode resistance, and tolerance to waterlogging. Additionally, peach, almond, peach–almond, and peach × *P. davidiana* hybrids have been used as a different source of nematode resistance, tolerance to iron-chlorosis, drought, replant problems, and compatibility with peach.

Within the USA, considerable efforts are devoted to develop a resistant or tolerant rootstock to the peach tree short life (PTSL) syndrome in the southeastern USA and the bacterial canker complex (*Pseudomonas syringae* pv. *syringae* van. Hall) in California, both of them linked with the ring nematode (*Mesocriconema xenoplax* (Raski) Loof & deGrosse). Research to find resistance to other harmful nematodes of the peach industry, such as the root lesion (*Pratylenchus vulnus* Allen and Jensen and *Pratylenchus penetrans* Cobb) and dagger (*Xiphinema americanum* Cobb) nematodes, is in progress because finding a broadly adapted and nematode-resistant rootstock that is also compatible with peach has been unsuccessful until now (Reighard and Loreti 2008). Rootstocks are also being developed for replant sites to reduce incidence of perennial canker (*Leucostoma* spp.) and the bacterial canker (*Pseudomonas syringae*) complexes found in peach production regions having light textured soils.

6 Breeding Methods and Techniques

6.1 Major Traits in Peach Scion Breeding

Adaptation is key in the development of consistently high-yielding cultivars. All breeding programs select for various adaptation traits as they select among their progenies for high bud density and fruit set.

Final productivity is dependent on several major adaptation traits: chilling and heat requirements, heat and cold tolerance, and resistance/tolerance to various biotic (disease and pest) and abiotic stresses.

Bloom time for peaches is determined by both the chilling and heat requirements of the flower buds. Given that the bloom order of peaches is consistent from year to year and over environments (Scorza and Sherman 1996), the most important determinant of

bloom time is the chilling requirement, although there are some peaches that require more heat to bloom than the majority (Byrne et al. 2000; Citadin et al. 2001; 2003).

Lower chilling requirement is a priority trait for a significant number of breeders. This trend toward lower chilling cultivars is evident in the fact that 50 years ago 90% of the peach cultivars required more than 800 chilling hours to break dormancy, whereas now only 20% of new cultivars require this much chilling (Sansavini et al. 2006). This has occurred inadvertently as breeders selected early ripening cultivars with the largest fruit size which tended to be the lowest chill and earliest blooming as well as purposely selected cultivars adapted to warmer regions or protected culture to expand the production zone of peach. This selection is best done in a low-chill zone as opposed to selecting early blooming (and presumably lower chill) selections in a high-chill zone as in many low-chill zones the warmer temperatures during the dormant and bloom periods dramatically change the fruit quality especially with respect to fruit size and shape (Topp and Sherman 1989; Byrne et al. 2000; Byrne 2010; López et al. 2007). Research into low-chill cultivars has been accelerated recently by the increasing emphasis put on a year-round supply of produce. This is possible with lower-chill cultivars with short development periods and complementary production in both the northern and southern hemispheres (Byrne 2005). Very late ripening cultivars also play a role in this goal.

Chilling requirement as estimated by bloom dates is a moderately to highly heritable (Souza et al. 1998a, 2000; Mowrey and Sherman 1986; Hansche et al. 1972; Hansche 1990). Thus breeders can achieve rapid genetic gain through selection of parents based on phenotype and recurrent mass selection (Topp and Sherman 2000). Low-chill cultivars have prompted most of the interest of peach breeders working in warm environments, starting from southern China germplasm in the late 1940s (Byrne et al. 2000; Byrne and Bacon 1999; Byrne 2003; Topp et al. 2008). Breeding in low-chill regions implies selecting against some common problems such as excessive blind nodes (Boonprakob et al. 1994, 1996; Richards et al. 1994) and bud drop and poor fruit shape which are traits whose expression is amplified by the inconsistent winter chilling and warm spring conditions frequently experienced in the low-chill zones (Byrne 2010). Breeding for low chilling in the last few decades has allowed the peach to be cultivated in many subtropical regions, from the southern states in the USA to Brazil, southeast Asia, Australia, South Africa, and most of the countries facing the warmest shores of the Mediterranean basin (Topp et al. 2008; Byrne et al. 2000; Sherman and Lyrene 2003; Raseira and Nakasu 2006).

High temperatures during bloom can have a negative effect on fruit set and consequently yield. Reports indicate that night temperatures above 15–18°C and day temperatures above 22–25°C are detrimental to fruit set in low-chill peach cultivars (Edwards 1987; Rouse and Sherman 2002b; Couto 2006; Couto et al. 2007). Recent work in Japan with the high-chill cultivar “Hakuho,” indicated that as the temperature was raised during flowering from 15 to 30°C, there was a decrease in percent pollen germination, flower and ovule size, and fruit set. The most abrupt changes occurred between 20 and 25°C (Kozai et al. 2002, 2004). In addition, cultivar differences are evident in the tree’s ability to set fruit under warm bloom time conditions (Rouse and Sherman 2002b; Couto et al. 2007). As low-chill cultivars are developed,

it is important to select them for their tolerance to high temperatures during bloom, as good tolerance to this stress will allow for more consistent production. This is especially important in the warmest production areas but also in areas where peaches can be produced in protected culture, double cropping or forced cropping systems (George et al. 1988; Sherman and Lyrene 1984; Jiang et al. 2004; Byrne 2010). An ability to set under a wider range of temperature conditions would give the producer more flexibility in the timing of the harvest seasons.

Tolerance to freezing temperatures during bloom can also be an important objective in some breeding programs in regions that are subject to crop losses from spring frost and/or freezes during bloom. Several approaches are possible to obtain cultivars tolerant to bloom freezes: late blooming, high bud density, and inherent bud resistance to colder temperatures. The first two approaches are avoidance approaches and represent traits that are moderately to highly heritable (Souza et al. 1998a; Citadin et al. 2003). Thus late blooming cultivars with high bud set have been developed. Unfortunately, little is known about the genetic variation of inherent resistance of deacclimating flower buds transitioning out of dormancy to freezing temperatures.

Extreme low temperatures represent a limiting factor in plant survival (Quamme and Sushnoff 1983). Consequently, breeding programs in cold regions, especially in the northern hemisphere, are focused on developing peaches with greater winter cold hardiness, which extends peach cultivation to higher latitude zones (Callahan et al. 1991). Peach flower and vegetative buds of some cultivars can withstand -30 and -35°C , respectively (Layne 1984). Hardy parents should be chosen among those accessions whose resistance to winter cold is consistent over rootstock, soil and temperature fluctuations, as reported in some Chinese germplasm. However, attention should be paid to bloom time of these accessions to eliminate early blooming progeny that would be susceptible to spring frost damage (Layne 1982, 1984).

Since hardiness is a quantitative trait (Mowry 1964), resistance to low temperatures would be improved by crossing very hardy parents with commercial peaches, and then selecting within the F_1 progeny followed by back crossing to improve fruit quality of the most hardy selections. Selection strategies for developing hardy peaches, other than relying on test winters and assessing the degree of twig xylem and dieback (Myeki and Szabó 1989; Layne 1982; Szabó 1992), are based on artificially induced low temperatures in portable field chambers or in a cold chamber on winter dormant potted trees (Stushnoff 1972; Quamme and Sushnoff 1983). The threshold of resistance (lowest temperature killing the flower bud) is checked directly or by methods such as exothermal analysis in which death is determined by the sudden temperature rise at the bud base, corresponding to ice formation in bud tissue. Alternatively, the cold treatment could be applied on 1-year old shoots harvested in mid winter. This is more efficient when assessing large progenies. Interestingly, hardy peaches usually possess high flower bud density (Werner et al. 1988), a possible mechanism for spring freeze avoidance (Byrne 1986) even in low-chilling peaches (Sherman and Lyrene 2003).

Disease and pest resistance. The consumers' concern about chemical residues on fruits and vegetables has increased considerably. Numerous disease organisms and pests attack peach and nectarine cultivars. Some, such as the brown rot, are of

worldwide distribution, whereas others have regional importance (Scorza and Sherman 1996; Byrne et al. 2000). Breeding programs all over the world, especially the ones located in humid areas have disease resistance as one of their top priorities. The lack of good known resistance sources and the fact that little is known about the inheritance of the disease and pest resistance of peaches is limiting the advances toward this objective.

One of the most serious diseases of peach worldwide is brown rot (*Monilinia fructicola* (Wint.) Honey and *M. laxa* (Aderh & Rull) Honey). Despite its importance, there has been relatively little work done on the development of brown rot resistant stone fruit cultivars because a small infection to the fruit results in complete loss of that fruit and so far the disease has been reliably controlled by fungicides. Nevertheless, several breeders (Brazil, California, Italy, and USA) either individually or associated with pathologists have concentrated efforts on obtaining new cultivars resistant to this pathogen. There are numerous reports of resistance (feral Mexican and Brazilian peaches) or tolerance (peaches from Florida, New Jersey, and Harrow programs) to fruit brown rot (*M. fructicola*) within peach (Feliciano et al. 1987; Scorza and Okie 1990; Scorza and Sherman 1996; Byrne et al. 2000). In general, the level of resistance reported is low to moderate and the screening techniques are not highly reliable. The Brazilian cv. Bolinha is considered to have a certain level of horizontal resistance to *M. fructicola* (Feliciano et al. 1987) as do a few newer Brazilian selections (Wagner et al. 2005a). However, the resistance is only in the epidermis (Gradziel et al. 1997; Lee and Bostock 2007), thus any disruption (such as insect damage) of the skin, will allow the fungus penetration and disease development.

In tests done in Italy, the level of resistance to fruit rot caused by *M. laxa* was assessed in 27 peach and nectarine cultivars. Of these, only four ('Contender,' 'Glohaven,' 'Maria Aurelia,' and 'Maria Bianca') had less than 60% diseased fruits. 'Contender' also had very high level of field resistance and when crossed to very sensitive cultivars (e.g., 'Elegant Lady') yielded seedlings more resistant than itself (Bassi et al. 1998). Artificial inoculation on unwounded fruits was found to be a reliable method in evaluating for brown rot (field) resistance, although the procedure is lengthy and affected by season and year variability.

Beyond attacking the developing fruit, this pathogen also attacks young shoots and flowers. The breeding work in southern Brazil (Pelotas, Rio Grande do Sul) selects for resistance to flower blight in their field plots. Although differences in the level of resistance to flower blight is seen, there seems to be no correlation between flower and fruit resistance and selection needs to be done for flower blight as well as for fruit reaction (Wagner et al. 2005b).

Bacterial leaf spot (*Xanthomonas arboricola* pv. *pruni*) is a disease particularly important in areas of high humidity accompanied by wind and sandy soils. Since chemical control efficacy is not always high, several breeding programs in Brazil, South Africa, and the USA have routinely selected for resistance to bacterial spot in peaches. Little is known about the genetics of resistance to this disease; however, Sherman and Lyrene (1981) suggested that resistance was controlled by a few major genes.

Cultivars of peach vary widely in their resistance to bacterial leaf spot with the more resistant cultivars being developed in humid areas (south and eastern North America, Brazil, and South Africa) where screening is done in the field with the existing pathogen pressure. Unfortunately their resistance may differ dramatically in different geographic regions (Byrne et al. 2000) due to unique pathogenic races of the bacteria (du Plessis 1988; Martins 1996) in different geographic regions. This makes the development of stable resistance to bacterial spot more difficult.

Other wide spread fungal diseases subject to some breeding or selection efforts are peach leaf curl (*Taphrina deformans* (Berk.) Tul.), rust (*Transchelia discolor* (Fuckel) Transchel & Litv.) (Pérez et al. 1993; Rouse and Sherman 2002a; Topp et al. 2008), and powdery mildew (*Sphaerotheca pannosa* (Wall. FR. Lev.); *Podosphaera pannosa* (Wallr.:Fr.) Braun & Takamatsu) (Rodríguez et al. 1992; Pérez 1997; Pascal et al. 2010). The most studied of these diseases are peach leaf curl and powdery mildew which are both cool season pathogens. These are generally adequately, but not always, controlled by a few sprays per growing season. Given the biology of the two fungi, in vitro or artificial inoculation is not easy to do and selection must rely on natural infection, either on the young seedlings in the green house or in the field.

Resistance to peach leaf curl is determined by a polygenic system (Ritchie and Werner 1981; Monet 1985; Viruel et al. 1998). Various sources of resistance have been reported, e.g., the peach seedlings ‘GF 305,’ ‘Redhaven,’ and ‘Cresthaven’ (bearing up to 50% of resistant seedlings in their progeny (Todorovic and Mistic 1982), the Italian white fleshed “Cesarini” (Bellini et al. 1993) and *Prunus davidiana* (Pisani and Roselli 1983).

The inheritance of powdery mildew resistance varies with its source. It has been described as a single dominant gene from the peach ‘Pamirskij 5’ (Pascal et al. 2010), to two loci, one controlling high resistance, the other medium and low resistance from *P. ferganensis* (D’Bov 1975) and polygenically from other peach cultivars (Pérez 1997) and *P. davidiana* P1908 (Dirlewanger et al. 1996). For the latter parent (Pascal et al. 1997), resistance has been introgressed to peach and molecular markers for various QTLs for resistance useful in selection have been identified (Foulongne et al. 2002, 2003a). Although the eglandular leaf phenotype is associated with a strong susceptibility to powdery mildew (Rivers 1906; Saunier 1973), both globose and reniform accessions can also show high susceptibility to this pathogen (Rodríguez et al. 1992). The results from greenhouse screening and field screening for powdery mildew resistance are both equally reliable (Rodríguez et al. 1992; Pérez 1997).

The major virus issue for the European peach and other stone fruit industry is the Sharka disease caused by the Plum Pox Virus (PPV) and transmitted by grafting and several species of very mobile aphids with the green peach aphid (*Myzus persicae* (Sulz.)) among the most important. It was originally described on peach in Greece and now it is reaching a pandemic diffusion in several peach growing countries in Europe and elsewhere (e.g., the USA and Canada). Breeding has been challenging because the assessment for resistance to PPV is a very lengthy procedure and requires artificial infection in insect-proof environments (either screen houses or

isolated places with no *Prunus* trees or possible source of PPV infection). Progeny to be tested have to be budded on test rootstocks, e.g., 'GF 305' peach seedlings, to check for possible tolerance mechanism (plant infected but without symptoms). If no symptoms appear on either the rootstock or scion over at least three vegetative cycles, ELISA followed by a PCR test are run to check for possible low concentrations of the virus (Rubio et al. 2009).

Although field resistance and tolerance to PPV has been reported in peach, the best source of resistance found is from a related species, *Prunus davidiana* which is being incorporated into peach by several Italian and French institutions. Resistance to PPV from *P. davidiana* is conditioned oligogenically and is syntenic to PPV resistance in apricot (*P. armeniaca* L.). Recently, QTLs associated with PPV resistance have been mapped, which should facilitate the development of a marker-assisted selection (MAS) approach (Foulongne et al. 2003b; Quilot et al. 2004; Decroocq et al. 2005; Bassi 2006) although this may be complicated by the report that not all the QTLs are stable over all the genetic backgrounds tested (Rubio et al. 2010).

Peaches are attacked by a range of nematodes including root knot (*Meloidogyne* spp.), ring (*Mesocriconema xenoplax* (Raski) Loof & de Grasse), root lesion (*Pratylenchus* spp.), and dagger (*Xiphinema americanum* Cobb) nematodes. Of these, the most important are the root knot nematodes and the ring nematode (Reighard and Loreti 2008). The most extensive work has been done with the *Meloidogyne* species of root knot and several dominant resistance genes have been identified for resistance to *M. incognita* (Kofoid and White) Chitwood and *M. javanica* (Traub.) Chitwood, the two most important species (Sharpe et al. 1970; Yamamoto and Hayashi 2002; Gillen and Bliss 2005; Claverie et al. 2004a, b; Esmenjaud 2009). In addition, a gene conditioning a broad spectrum resistance has been identified in plum and is being used in rootstock breeding (Esmenjaud 2009). Furthermore, markers associated with these various genes for root knot nematode resistance have been identified and are being used for selection of resistant rootstocks (Lu et al. 1998; Wang et al. 2002a; Lecouls et al. 2004; Gillen and Bliss 2005; Esmenjaud 2009).

No clear resistance has been found to *Mesocriconema xenoplax*, a nematode associated with peach tree short life (PTSL). However, Guardian® rootstock is considered to be tolerant to the nematode, since it is less susceptible to peach tree short life and causes the scion to be less susceptible to cold injury and bacterial canker, the main causes of PTSL, than any other rootstock tested thus far (Okie et al. 1994). Screening for resistance to lesion nematodes (*Pratylenchus penetrans* (Cobb) Filipjev and Schuurmans Stekhoven and *P. vulnus* Allen and Jensen) among *Prunus* has shown a range of susceptibility in peach and a source of broad based resistance in plum (McFadden-Smith et al. 1998; Pinochet et al. 2000). Unfortunately, there was a wide range of pathogenicity among *P. vulnus* races which creates difficulties in breeding for resistance (Pinochet et al. 2000).

Thus far, no high level of resistance has been found to the oak root rot fungus (*Armillaria mellea* (Vahl: Fr.) P. Kumm. and *Armillaria tabescens* (Scop.) Dennis et al.) although there has been resistance reported in some plum rootstocks to *A. mellea* in Europe (Guillaumin et al. 1991; Jiménez et al. 2011) and plum germplasm

to *A. tabescens* in the USA (Beckman et al. 1998; Beckman 1998; Beckman and Pusey 2001). Unfortunately, some plum rootstocks reported as resistant to *A. mellea* were found to be susceptible to *A. tabescens*. The progress in the development of *Armillaria* resistant rootstocks is expected to be slow due to a lack of an excellent source of resistance and the long and tedious procedure needed to quantify their resistance (Beckman and Pusey 2001).

Even though peaches are attacked by several insect pests, few breeding programs work with insect resistance. The most active programs for insect resistance are those run by INRA in France and by the Centro di Ricerca per la Frutticoltura (CRA-FRU) in Italy. These programs focus on green peach aphid (*Myzus persicae*) resistance (Liverani and Giovannini 2000; Sauge 1998; Monet et al. 1998) because of its importance in Europe due to both the direct damage (leaf curl and stunting) it causes but also because it is the vector for Plum pox virus. Green peach aphid resistance has been described in three sources: a weeping peach tree (Weeping Flower Peach), *P. davidiana* and ‘Rubira’ rootstock (Massonie et al. 1982). This resistance is a hyper-sensitivity reaction to the aphid testing probe on young shoots or leaves which causes a necrotic zone to develop around the puncture hole, thereby isolating the neighboring leaf cells (Sauge 1998). A dominant mode of action for aphid resistance has been identified in the resistance from ‘Weeping Flower Tree Peach’ (Monet and Massoníé 1994; Monet et al. 1998; Monet 1985) and ‘Rubira’ (Pascal et al. 2002), although it is not known if these are allelic or not.

Resistance to abiotic stresses. Resistance to calcareous high pH soils is an important trait for peach production regions with calcareous soils found most commonly in semi arid and arid zones. High pH causes iron deficiency, which lowers leaf chlorophyll, fruit yield, fruit size and soluble solids content according to the degree of chlorosis (Razeto and Valdés 2006). Tolerance has been identified among peach, plum and particularly almond (Shi and Byrne 1995; Jiménez et al. 2008). Presently peach–almond hybrid rootstocks are commonly used in calcareous soils to ensure sufficient iron uptake by the plant (Reighard and Loreti 2008). Selection procedures include field evaluation in calcareous soils, greenhouse evaluation at various levels of bicarbonate (Shi and Byrne 1995) and most recently via laboratory measurements of root iron reductase activity on hydroponically grown plants (Jiménez et al. 2008).

A soil pH below 5.5 is deleterious to peach tree growth, fruit yield and size, and tree longevity. There is an improved performance of trees when soil pH is maintained above pH 6.0. Deleterious effects of soil pH below 5.5 may be related to the toxicity of Al or low Ca availability (Cummings 1989). Unfortunately, no source of tolerance to aluminum toxicity has been identified (Chibiliti and Byrne 1989). Consequently, this issue is managed by lime application to raise the soil pH.

Peach seedling rootstocks are not tolerant to waterlogging and thus grow poorly or die when planted in even seasonally waterlogged soils. The intensity of the waterlogging effect is more pronounced if the plant is actively growing as compared to dormant trees. The difference in flooding tolerance found among *Prunus* species other than peach is based on complex anatomical processes such as aerenchyma formation and biochemical adaptation involving the fermentative pathways to obtain

energy. Several candidate genes have been identified to be involved in the tolerance in two *Prunus* genotypes (Amador et al. 2009; Amador 2010). Various plum and interspecific hybrids have been reported to be tolerant of waterlogged soils (Table 14.2; Moreno 2004; Reighard and Loreti 2008).

Tree architecture. Peach productivity is relatively low and pruning costs are relatively high as compared to other tree fruit such as apples. Higher production efficiency could be obtained with higher cultivation density using modified growth types and dwarfing rootstock. Several breeding programs have worked toward the development of growth habit modification to increase yields with decreased management costs. There are a number of mutations differing from standard growth that could be exploited, ranging from brachytic dwarf to weeping and columnar (pillar) (Bassi 2003; Fideghelli et al. 1979; Mehlenbacher and Scorza 1986; Scorza et al. 1989). Interestingly, some interaction occurs between phenotypes, thus several intermediate growth architectures can be obtained (Bassi and Rizzo 2000; Scorza et al. 2002; Werner and Chaparro 2005; Hu and Scorza 2009). Given the simple inheritance of these traits, selection for a given tree structure is easily performed in one or two generations, depending on the dominance of the trait sought (Monet and Bassi 2008). Since segregation will occur for all of the other traits, several cycles of recurrent selection has to be applied to recover the commercially useful fruiting phenotype. Some recent commercially available introductions are already featuring growth habits different from the standard growth such as the upright ‘Sweet-N-UP’ and the columnar types ‘Crimson Rocket’ and ‘Alice-col’ (Liverani et al. 2004; Scorza et al. 2006).

The modifications for controlling size of trees necessary to satisfy the criteria for modern fruit-culture are aimed at smaller plants more suitable for high density plantings and reduction of the pruning needed to promote new fruiting wood in peach (Scorza and Sherman 1996). However, while these strategies have been largely successful in the apple industry, the peach tree seems more recalcitrant, probably due to the positive relationship between branch or tree vigor and fruit size (Manaresi and Draghetti 1915; Marini and Sowers 1994; Moreno et al. 1994). Although most dwarfing rootstocks for peach runted the trees and negatively affected fruit size, they did generally induce better peach fruit organoleptic quality (Albás et al. 2004; Mathais et al. 2008). Work continues to develop rootstocks that induce precocity, larger fruit size and quality as well as yield.

Fruit traits. The harvest season in the major production zones of the northern hemisphere can range from mid-April to mid-November (Llácer et al. 2009). However, extension of the harvest season remains an important trait in many programs in different growing regions due to market opportunities (Raseira et al. 1992; Byrne et al. 2000) and because of the quality deficiencies of existing cultivars at the extremes of the harvest season (Scorza and Sherman 1996). Various studies on the inheritance of the ripening time and fruit development period (FDP) have shown that these traits are highly heritable and mainly additive though there is evidence of a few genes with relatively large effects (French 1951; Bailey and Hough 1959; Souza et al. 1998a; Yu et al. 1997). Consequently, rapid genetic gains for short FDP are possible

in breeding programs (Hansche et al. 1972), though this is limited by a negative genetic correlation with fruit size and fruit quality (Souza et al. 1998b).

Large fruit size is also an important goal in most peach breeding programs. Furthermore, the achievement of large fruit size is more difficult in germplasm with short FDP (Souza et al. 1998a, b, 2000) and in regions with warm temperatures during fruit development (Topp and Sherman 1989; López, et al. 2007). Thus it is an especially challenging objective in warm subtropical and tropical production zones where early ripening is also a major objective (Byrne et al. 2000). Fruit size is a polygenic trait with a low to moderate heritability (Souza et al. 1998b; Hansche et al. 1972) due to the large influence that environment conditions, plant nutrition, and cultural practices (pruning and thinning) have on its expression.

Fruit firmness is essential for efficient handling and marketing. Whereas most fresh market peach breeding programs have traditionally emphasized the development of melting flesh type fruits, some such as the Brazilian (Pelotas), Mexican, and Spanish programs and more recently, Florida and some California programs, in the USA, have worked with nonmelting types. These genotypes are firm enough to harvest at a more mature stage, which allows for better quality (Brovelli et al. 1995, 1998; Beckman and Sherman 1996; Robertson et al. 1992) and larger size. Examples of this are ‘Eldorado,’ ‘Maciel,’ and ‘Granada’ in Brazil (Raseira and Nakasu 2003), ‘UFPrince,’ ‘Gulfking,’ ‘Springprince,’ ‘Springbaby,’ and ‘Crimson Lady’ in the USA (Byrne 2005), and ‘Calante,’ ‘Evaissa,’ ‘Jesca,’ and ‘Miraflores’ in Spain (Bouhadida et al. 2007a; Espada et al. 2009). The melting (M) and nonmelting (NM) flesh types are controlled by four alleles at the *F* locus. The nonmelting clingstone trait is recessive to the various melting flesh types (Peace et al. 2005, 2007; Monet 1989).

Another type of flesh with potential in the development of firmer freestone peaches with tree ripe flavor and longer storage life is the stony hard (SH) flesh found in cultivars such as ‘Jingsu’ from China (Byrne 2005), ‘Yinggetao’ from Taiwan (Lu et al. 2008), ‘Hakuto’ from Japan and ‘Yumyeong’ from Korea (Liverani et al. 2002; Haji et al. 2005). It is a monogenic recessive trait (Yoshida 1976; Haji et al. 2005; Liverani et al. 2002) that gives the fruit a very firm crunchy flesh which ripens more slowly due to suppressed ethylene production (Hayama et al. 2006). The stony hard trait is inherited independently of the melting flesh/nonmelting flesh trait and is epistatic to this trait (Haji et al. 2005). Unfortunately, it is difficult to identify in the field thereby making reliable selection difficult. Examples of cultivars with stony hard flesh are three of the ‘Ghiaccio’ series of peaches developed in Italy, which were selected from a open pollinated population of ‘Yumyeong.’ They all have sparse pubescence, white flesh (with a red vein in ‘Ghiaccio 22’), juicy but very firm flesh, with a texture similar but not equal to a clingstone peach, and good flavor with high sugar content (Nicotra et al. 2002).

Within the melting texture there is a very interesting phenotype, resembling the SH flesh in firmness and crispiness, but becoming melting when fully ripe and showing a prominent delay in softening, and ethylene production. This flesh texture is found in recently developed cultivars, both nectarines (e.g., ‘Big Top’) and standard peaches (e.g., ‘Rich Lady’ and ‘Diamond Princess’). Its remarkable keeping

quality, particularly on tree, is of primary importance for both growers and consumers. However, it is very difficult to assess on the tree when scoring segregating progenies, as is the SH flesh phenotype. The physiological basis and inheritance of this trait are being actively investigated (Tatsuki et al. 2006; Begheldo et al. 2008).

Flesh color varies in peach, from white to yellow to dark red, with variations in tonalities, greenish-white, light yellow, orange yellowish, and orange (Cevallos-Casals et al. 2005; Vizzotto et al. 2007). Traditionally white flesh peaches were preferred in Asia and in some European countries (e.g., France, Italy) until the 1960, and yellow-fleshed peaches preferred in the Americas and Europe, but recently, there has been an expansion of the use of white-fleshed peaches and nectarines in non-Asian markets. Thus, several programs outside Asia have worked intensively to develop white flesh peaches and nectarines for the American and European markets (Argentina, Brazil, Italy, Taiwan and in the USA the programs of Arkansas, California, Georgia, North Carolina, Texas, among others). White flesh is dominant over the yellow (Connors 1920), but there are variations in tonalities of white as well as yellow.

Blood flesh peaches and nectarines are sought in breeding programs in France (T. Pascal, personal communication), the USA (Okie 1988; Vizzotto et al. 2007; Cevallos-Casals et al. 2005), China (R. Ma, Nanjing, personal communication), Italy, and Spain (Cantín et al. 2009b) for their novelty and potential health benefits of the enhanced levels of anthocyanins (Vizzotto et al. 2007; Cantín et al. 2009b). Both of the sources of this blood flesh trait appear to be inherited independently of yellow/white flesh color locus. Most of this breeding has thus far worked with the recessive blood red gene which was characterized from 'Harrow Blood' and many landraces in France and Italy. This gene induces the early development of anthocyanin in the fruit pulp beginning at the pit hardening stage and is associated with red leaf veins (Werner et al. 1998; Gillen and Bliss 2005). Another source of red flesh in peach has been found in China (T. Pascal, personal communication) and among some local peach selections in Georgia (W. R. Okie, personal communication). This red flesh trait, which appears to be inherited as a dominant trait, is characterized by a late anthocyanin development in the mesocarp and is associated with green veins. On the other extreme, Italian breeders have released two cultivars, 'Ghiacco 1' and 'Ghiacco 3,' without any anthocyanins (Nicotra et al. 2002).

Skin color is not important for cultivars used in the processing industry; nevertheless it is a very important component of appearance when the fruits are produced for fresh market. Most European and American markets prefer a red over color superior to 80% of the skin surface, whereas other markets such as in Asia, Brazil, Mexico, and Spain accept fruit with less than this and even 20% red blush over a bright yellow or white background are well accepted by consumers. In a few specific markets with nonmelting flesh peaches in southern Brazil and parts of Mexico, southern Italy, and Spain, a completely yellow skin associated with nonmelting flesh is preferred. A skin and flesh cream-yellow uniform color is preferred in the very late ripening cultivars grown in the Ebro Valley in Spain (Espada et al. 2009). This peach industry is based on high quality nonmelting fruits individually bagged during their development on the tree.

The expression of a red skin color is difficult to categorize and has a high degree of environment interaction especially with respect to light exposure (altered by climate, growth, position of the fruit in the canopy and pruning practices) and nutrition (Luchsinger et al. 2002; Trevisan et al. 2008). Red skin color is generally controlled by multiple gene action (Hansche 1986; Scorza and Sherman 1996; Souza et al. 1998b) although there also appears to be several qualitative recessive genes controlling skin color: one controlling full red skin color, even on shaded portions of the fruit surface in some germplasm (Beckman and Sherman 2003) and another that suppresses red skin color (Beckman et al. 2005).

Fruit shape is an important fruit quality attribute, since it influences consumer's acceptance and postharvest handling. In addition, protruding tips and sutures can be bruised during handling and shipping of fruit and are, therefore, undesirable traits for commercial peaches (Kader 2002). Fruit shape is moderately heritable (Souza et al. 1998b), but is also influenced by the temperatures during winter and/or early fruit development with warmer temperatures conditioning the development of larger tips and more irregular shapes (Topp and Sherman 1989; Byrne et al. 2000). This represents a production problem especially under tropical and subtropical conditions. Breeding programs have been selecting for rounder shapes and some new cultivars, even in the subtropics, no longer have the problem, such as the cv. 'Rubimel,' released by Embrapa in 2007, that has a very small or no tip, even when cultivated at 23–24° latitude in São Paulo State, Brazil.

Some of the most common complaints by consumers are the presence of off flavors, flesh mealiness, flesh browning and black pit cavity due to IB (Crisosto 2002) and inconsistent quality in stone fruit (Byrne 2005). This is, in part, related to the production techniques which emphasize yield and inadequate postharvest handling protocols but also to the cultivars produced by breeders who focused on external quality at the expense of internal quality. Recently, many breeding programs have shifted their focus on increasing the internal quality of the cultivars that they develop. Although peach flavor is quite complex and preferred profile varies with regional and personal customs (Crisosto et al. 2006), the major easily measured traits are the sugar (total soluble solids, total sugars, sucrose, fructose, glucose, and sorbitol) and acid content (titratable acidity, malic, citric, quinic, and shikimic acids) as well as the ratio between these (Colaric et al. 2005; Crisosto et al. 2006; Cantín et al. 2009a).

Peaches are expected to be sweet and to be readily accepted by consumers, acid and low-acid fruits need to have more than 10 and 11°Brix of soluble solids content (SSC), respectively (Crisosto and Crisosto 2005). Currently, there are selections and cultivars with fruits close to or even higher than 20°Brix such as some nectarines from the private and USDA programs in California and the 'Ghiaccio' series in Italy. Total SSC has a low to moderate heritability, which should allow steady improvement of fruit sugar levels in spite of the variations caused by environmental, maturity, and production differences between regions and years (Cantín et al. 2009a). Although many mid- and late-ripening cultivars already have these minimum levels of SSC, they can be improved. Unfortunately, this process will be more

difficult with early ripening genotypes with a very short fruit development period (FDP) due to an association between low FDP and low SSC (Souza et al. 2000).

The acidity levels in peach are controlled by both qualitative and quantitative genes (Connors 1920; Souza et al. 1998b). The dominant allele of gene D conditions low acidity (Connors 1920) and colocalizes with QTLs which affect pH, titratable acidity, and organic acid contents (Boudehri et al. 2009). These low-acid peaches have a higher pH (more than 3.9) and a total acidity 2–4 times lower than standard cultivars due to lower concentrations of citric, malic (about 50%), and quinic (about 20%) acids (Byrne et al. 1991; Brooks et al. 1993; Crisosto et al. 2006). The dominant nature of the low acid and the white flesh traits has made the conversion of superior acid yellow flesh materials traditionally preferred by many American and European markets into low-acid white genotypes preferred by many Asian markets and now with increasing popularity in American and European markets, a relatively easy process. In addition, the low-acid trait allows the earlier harvest of melting flesh fruit without affecting the taste, but if total sugars are below 11–12°Brix, then a very bland flavor is experienced (Crisosto et al. 2001, 2006).

High dietary consumption of fruits and vegetables particularly those with antioxidant activity has been linked to reduced risks of many chronic diseases including cancer and cardiovascular diseases (Wargovich 2000). The phytochemicals in stone fruit have been linked to inhibiting the development of cardiovascular disease and the growth of various cancers (Byrne 2007; Lea et al. 2008; Noratto et al. 2010) and may also extend the shelf life and reduce the incidence of diseases of fruits (Khanizadeh et al. 2007). There is a broad genotype variation in the content of these phytochemicals with some peach selections and many plums having a similar antioxidant activity as blueberry (Byrne et al. 2009; Vizzotto et al. 2007). The antioxidant levels were well correlated with total phenols although not necessarily with anthocyanin content of the fruits (Cevallos-Casals et al. 2005; Vizzotto et al. 2007; Cantín et al. 2009b). Thus far, no stone fruit cultivars have been developed specifically for higher levels of these phytochemicals; however, such cultivars would provide a new product that could be sold fresh or processed into extracts (Byrne 2005). This possibility has guided peach breeders to consider antioxidant compounds and other nutritional properties as interesting targets in breeding programs (Cevallos-Casals et al. 2005; Vizzotto et al. 2007; Cantín et al. 2009b). More research in the health effects of various stone fruit phytochemicals is needed to better define the specific phytochemicals and the quantities desired.

Poor postharvest quality due to the harvesting of hard unripe fruit and IB, a fruit disorder that develops in cold storage, is the main limitation to the marketing of some peach cultivars. Although the symptoms of IB (e.g., mealiness, flesh browning, loss of flavor, and bleeding) can be minimized by storing below 5°C, ethylene application or intermittently raising the temperature during cold storage or by preconditioning fruit prior to storage or shipping, the best approach is to breed cultivars resistant to it (Crisosto et al. 1999; Crisosto 2006; Peace et al. 2006; Cantín et al. 2010b). We know little about the inheritance of IB, but it appears that only a few genes control each of the symptoms (Peace et al. 2006). Given the fact that it is

expensive to measure a genotype's susceptibility for IB (Crisosto et al. 1999), there is considerable work trying to identify molecular markers associated with these traits (Peace et al. 2006; Ogundiwin et al. 2009; Cantín et al. 2010b). Although the evaluation techniques for postharvest traits are cumbersome, much emphasis has gone to these objectives. In the development of fresh market cultivars, there is also considerable effort to incorporate nonmelting flesh to increase fruit firmness, which may have the additional effect of improving resistance to IB as peaches with non-melting flesh tend to be more tolerant to IB than those with melting flesh (Brovelli et al. 1998; Crisosto et al. 1999; Peace et al. 2006).

6.2 *Breeding Methods and Techniques*

Although the difficulties related to fruit tree genetics (long generation time and large plant size) have slowed genetic investigations on fruit crops, much information on character inheritance has been collected for peach. This is because this species has a shorter generation time and smaller plant size than other major fruit crops, as well as has a small chromosome number, is self-fertile, is tolerant of inbreeding depression, and many important qualitative traits are transmitted according to simple Mendelian inheritance. Mendelian traits in peach, association to specific genomic linkage groups and the estimates of heritability of major quantitative traits have recently been reviewed (Monet and Bassi 2008). Quantitative genetics considers continuously variable traits such as fruit size, fruit skin color, firmness, and taste that are both polygenic and influenced by environment factors (multifactorial traits) and consequently they are more difficult to improve because their level of heritability is relatively low.

In the last century thousands of novel cultivars have been released especially in the USA and Europe. Most of them come from cross breeding, either via controlled crosses (~50%) or via open pollination (~20%) and only around 4% from bud sports (Della Strada et al. 1996). Other possible breeding techniques are somaclonal variation, mutation breeding, and transformation.

Intraspecific crossing is the most common method for peach breeding and still continues to supply the vast majority of the new cultivars worldwide. Variable strategies may be followed according to the available germplasm and goals.

Highly valuable cultivars derive either from self-pollination or from crossing between related parents. This strategy allows the combination of several quantitative traits of horticultural and market importance. It is well known that despite of the very few genotypes used at the origin of peach breeding in the USA and the high degree of inbreeding, most of the cultivar improvement comes from this apparently small gene pool (Scorza et al. 1985) and a continued improvement of quality traits have been made in spite of this high degree of inbreeding. In part, this continuous improvement is due to outcrossing breeding populations with unrelated genotypes to incorporate desirable characters, such as fruit quality, diverse chilling requirements, and pest or disease resistance (Cantín et al. 2010a).

Since peach is tolerant to inbreeding depression (Lesley 1957; Monet and Bassi 2008), it is possible to develop seed propagated genotypes that would breed true-to-type, which is essentially what has been done in the development of seed propagated rootstocks as well as fruiting cultivars in Central America (Pérez 1989). Beyond the ease of handling seed versus budded trees, another advantage of seed propagated cultivars would be the freedom from diseases as most are not transmitted via pollen or seed. It has also been suggested that inbred lines could be developed via several generations of selfing or by doubling haploid lines (Hesse 1971; Toyama 1974; Scorza and Pooler 1993) to create seed propagated hybrids as is done with maize. Unfortunately, a lack of a heterotic effect (Monet and Bassi 2008) would make this approach less useful.

When the desired characters are not to be found within the breeding populations of *P. persica*, related species are employed, usually for incorporating oligo- or monogenic traits. For scion cultivar breeding, the two species worked with most are *P. davidiana* and *P. dulcis*. *P. davidiana* has been used as a donor for resistance to green peach aphid, powdery mildew, peach leaf curl, and PPV (Viruel et al. 1998; Sauge 1998; Foulongne et al. 2003a, b; Decroocq et al. 2005; Rubio et al. 2010), whereas in almond the focus is on the introgression of genes for kernel quality, drought resistance, growth habit (e.g., spur bearing), low bruising, flowering habits of cleistogamy, and resistance to some diseases into peach germplasm (Martínez-Gómez et al. 2004; Gradziel 2003). Although there are few fertility barriers in developing these hybrids and creating subsequent breeding populations, several generations of backcrossing are needed to restore fruit quality (Foulongne et al. 2003b; Pascal et al. 1997).

In breeding for rootstocks, the selection for the desired trait(s) could be pursued within the F_1 progeny and the high level of heterozygosity, sometimes involving floral sterility, does not hamper clonal propagation. Consequently, interspecific hybridization with related species for useful traits such as tolerance to calcareous or droughty soils (almond), nematode resistance (*P. davidiana*, various plum species), waterlogging tolerance (various plum species) and dwarfing (various plum species) is quite common (Table 14.3; Reighard and Loreti 2008; Bouhadida et al. 2007b).

6.3 Breeding Methodology

Criteria for choosing the best parent are particularly critical. While traits under simple Mendelian inheritance can be easily traced within a given progeny and through generations, quantitative traits, controlled by polygenic systems, require a different approach.

Parents may be superior to commercial cultivars characterized by high productivity and fruit quality. This method is simple, fast and offers a good chance to get desired combinations, but the repeated use of the best cultivars as parents leads to high phenotypic homogeneity. In other cases an advanced selection based on one or more useful traits, such as those related to specific resistance or fruit quality, is chosen

Table 14.3 Single gene traits described in peach and their position on the *Prunus* reference map^a

Character	Gene ^b	References	LG ^c
<i>Tree</i>			
Anthocyanins/anthocyaninless	An/an	Monet (1967)	
Normal/albino (no chlorophyll)	C/c	Bailey and French (1949)	
Tall, normal/pillar (broom)	Br /br or Pi/pi	Lammerts (1945)	G2
Tall, normal/bushy	Bu1/bu1 Bu2/bu2	Lammerts (1945)	
Normal shape/compact shape	Ct/ct	Mehlenbacher and Scorza (1986)	
Tall, normal/brachytic dwarf	Dw /dw Dw2/dw2 Dw3/dw3	Lammerts (1945) Hansche (1988) Chaparro et al. (1994)	G6
Normal shape/weeping shape	Pl/pl We/we	Monet et al. (1996) Chaparro et al. (1994)	
<i>Leaves</i>			
Leaf color (red/green)	Gr /gr	Blake (1937)	G6–G8
Glandular/eglandular	E/e	Connors (1922)	G7
Deciduous/evergreen	Evg /evg	Rodríguez et al. (1994)	G1
Leaf shape (narrow/wide)	Nl /nl	Yamamoto et al. (2001)	G6
Leaf margin (smooth/wavy)	Wa/wa Wa2/wa2	Scott and Cullinan (1942) Chaparro et al. (1994)	
<i>Flowers</i>			
Single/double flower	Dl /dl	Lammerts (1945)	G2
Pollen (fertile/sterile)	Ps /ps Ps2/ps2	Scott and Weinberger (1944) Chaparro et al. (1994)	G6
Petal color (colored/white)	W/w	Lammerts (1945)	
Petal color (pink/red)	R/r	Lammerts (1945)	
Petal color (dark pink/light pink)	P/p	Lammerts (1945)	
Petal color (pink/pale pink)	Fc /fc	Yamamoto et al. (2001)	G3
Showy flowers size (large/small)	L/l	Lammerts (1945)	
Type (nonshowy/showy)	Sh/sh	Bailey and French (1949)	
<i>Fruit</i>			
Monocarpel/polycarpel	Pcp /pcp	Bliss et al. (2002)	G3
Anthocyanin (normal/blood flesh)	Bf /bf	Werner et al. (1998)	G4
Sweet fruit/normal fruit	D /d	Monet (1979)	G5
Freestone/clingstone	F /f	Bailey and French (1949)	G4
Pubescent skin/glabrous	G /g	Blake (1932)	G5
Saucer shape/nonsaucer	S /s	Lesley (1939)	G6
Nonaborting/aborting fruit	Af /af	Dirlewanger et al. (2006)	G6
Kernel (bitter/sweet)	Sk /sk	Werner and Creller (1997)	G5
Flesh color (white/yellow)	Y /y	Connors (1920)	G1
Skin color (red/green)	Sc /sc	Yamamoto et al. (2001)	G6–G8
Flesh color around stone (red/white)	Cs /cs	Yamamoto et al. (2001)	G3

(continued)

Table 14.3 (continued)

Character	Gene ^b	References	LG ^c
Flesh texture and pit adherence (F) ^d	M/m or F	Bailey and French (1933; 1949); Monet (1989); Peace et al. (2005)	G4
Melting freestone	F/-	Peace et al. (2005)	
Melting clingstone	f/f		
	f/f1		
	f/n		
Nonmelting clingstone	f1/f1	Peace et al. (2005)	
	f1/n		
	n/n		
Stony hard flesh (Hd)	hd/hd	Yoshida (1976)	
Stony hard, melting ^e	hd hd/F-	Bailey and French (1949); Haji et al. (2005)	
Stony hard, melting	hd hd/f ₁ f ₁	Haji et al. (2005)	
<i>Disease or pest resistance</i>			
<i>Myzus persicae</i> resistant/susceptible	Rm1/rm1	Massonie et al. (1982); Monet (1985)	
Powdery mildew resistant/susceptible	Sf/sf	Dabov (1983)	
<i>M. incognita</i> resistant/susceptible	Mi/mi	Weinberger et al. (1943)	G2
<i>M. javanica</i> resistant/susceptible	Mj/mj	Sharpe et al. (1970)	

^aUpdated from Dirlwanger and Arús (2005)

^bMapped genes in bold

^cLocated on T×E map; G6–G8 genes located close to the translocation breakpoint between these two linkage groups

^dFour alleles at the same locus controlling both flesh texture (endopolygalacturonase enzyme expression) and pit adherence; the fourth, null allele (n), has the same effect as the f₁ allele (non-melting clingstone) (Peace et al. 2005)

^eIndependent inheritance of this trait was demonstrated, also suggesting an epistatic influence on the F locus, since when exogenous ethylene is applied, the stony hard-melting (*hdhd/f-*) phenotype is induced to soften (Haji et al. 2005)

to introduce the desired trait into a commercially important cultivar. The choice of two parental individuals with complementary phenotypic characters has led to the improvement of most of the commercially important fruit characters (Monet and Bassi 2008). Data on the heritability of quantitative traits confirm that parents could be chosen on the basis of their phenotype to yield rapid gains (Hansche et al. 1972; Souza et al. 2000). However, if the expression of a given trait is influenced by dominance or epistasis, the choice of a parent on a phenotypic basis could be misleading and lead to a worthless progeny.

For the above reason, the genetic value of a given parent should be assessed through a progeny study (Monet 1995). The simplest way is to perform a self-pollination: the more heterozygous the progeny, the more heterozygous the parent. This method gives valuable information particularly on simple traits, unveiling recombination and recessive characters. However, for traits under polygenic control, the evaluation

of the prepotency, or combining ability, is better suited to rate the potential of a given genotype in yielding superior progenies (Fogle 1974). The simplest progeny test would be to compare several populations sharing a common parent (Cantín et al. 2009a, 2010a). The evaluation could involve one or more traits and has the advantage that could be done within a given breeding program design, thus not requiring additional studies or plantings.

The number of seedlings required for a given progeny may vary considerably. If segregation is sought for a genetic study on simple traits, just one or very few F_1 individuals are required to obtain an informative F_2 generation. If quantitative traits are to be studied, at least 100 seedlings per progeny are needed to assess variability and linkage relationships (e.g., when searching molecular markers for MAS), but larger numbers, around 1,000 seedlings, will assure sounder results. For heritability estimates, more than 100, even if small-sized, diverse progenies are needed to mimic the panmictic distribution of genes. For breeding purposes the progeny size for selecting new cultivars depends on the commercial cultivars already available, goals sought, and prepotency of the parents (Fogle 1974). Thus, an acceptable size of a progeny with a good probability to yield a new cultivar may vary from a few hundred to a thousand seedlings.

Given the size of the trees, it is common to do pollinations on trees in the field although some programs grow trees for breeding in large pots and move them in and out of a greenhouse for pollination. A major problem in the production of hybrid seed are cold temperatures during bloom which can be protected against by overhead sprinklers, orchard heating, or individual tree protection by covering with plastic films or fabrics and providing an heat source inside.

The hermaphroditic flowers of peach are easy to emasculate by cutting the calyx below the anther attachment with various notched sharpened devices, tweezers, or one's fingernails. This is done at the flower balloon stage, a few days before full bloom. In the case of exposed anthers of a nonshowy flower, it is important to check that the anthers are reddish and not dehiscing when the flower is emasculated.

For pollen, flowers at the balloon stage, before the anthers dehiscence, are collected and taken into the laboratory where the anthers are removed by cutting by hand or via rubbing the flowers either whole or cut in half transversely on a sieve. The detached anthers are allowed to dry at room temperature on an aluminum or paper tray or Petri dish for 24–48 h. Pollen needs to be maintained on a desiccant in cool conditions for current year use. Extra pollen batches or pollen collected for a next season pollinations can be stored desiccated at -18°C for 2–3 years or at -80°C for a longer time. Liquid nitrogen will ensure an almost indefinite storage.

Pollen is taken to the field in a vial, test tube or small jar. It is applied to the pistil with a pencil eraser, small camel hair brush, or one's finger tip and should be done either immediately or within 24–48 h after emasculation. Up to about 2 weeks after pollination the tree has to be checked for any unemasculated flowers that need to be removed to prevent the development of these unpollinated and probably self-pollinated fruit.

For normal breeding operations the flowers are generally not protected because emasculated flowers do not attract pollinating insects and peach pollen is heavy. If the progeny is to be investigated for genetic studies, a fine grid cage can be used

to protect the tree from pollen moved by insects or wind from the neighboring trees. An insect-proof cage, usually made from an 80–90% shading net, should be provided to protect the mother tree where self-pollination has to be made. Fruit set is improved when self-pollination is done by hand at full bloom. The cage can be removed after petal fall.

Fruits from pollinated flowers should be harvested when ripe and the seed extracted from the pit to facilitate seed germination. Peach seeds need stratification to overcome dormancy and thus to germinate fully developed plantlets. The chilling requirement is positively related to that of the mother tree (Pérez 1990). Seed coat removal can speed up germination, unless it should be kept to avoid cotyledons splitting before germination occurs. If chilling is not satisfied, germination would be delayed and rosetting will occur. Seeds should be stored at -1 to 1°C in sterilized moist sand, in perlite moistened with a fungicide solution, or in sealed Petri dishes with a filter paper disk wetted by a fungicide solution. After 1–5 months, or as soon as the radicle tip emerges from the seed when still in storage, they can be planted in the greenhouse. Higher stratification temperatures (up to 4°C), although equally effective in overcoming dormancy, may not be low enough to stop seed rot caused by bacteria or fungi that can develop in the cold room.

In temperate climates the seedlings are grown in the greenhouse during the winter, then either transplanted in a nursery plot or directly in the field the following spring although in some programs the seedlings are grown outside just after germination to reduce greenhouse-related disease problems. Seeds collected from low-chilling genotypes in warm winter regions that can be successfully stratified in 3–4 weeks and then germinated, can be grown large enough in the same season to transplant in the field the same year of the cross.

Viability is poor in early ripening genotypes (less than 100–120 FDP) and aseptic culture is needed to ensure germination (Tukey 1934). Generally, embryos with a seed dry weight of less than 30% need to be put through in ovulo and/or embryo rescue procedures for consistent seed germination success (Bacon and Byrne 2005). The fruits of these genotypes should be harvested well before full ripening, not later than the veraison stage, to avoid contamination from juice exposure or fruit rot. The smallest embryos (<5 mm in length and as young as 50 days of development) require 4–8 weeks of in ovulo culture to enlarge the embryos sufficiently before the embryos can be successfully rescued (Ramming 1985; Pinto et al. 1994). The larger embryos (>10 mm in length) are explanted after seed coat removal and placed in a sterile culture tube containing a suitable nutritive medium (i.e., sugars, minerals, and vitamins; growth regulators are usually not needed) (Ramming 1990; Sinclair and Byrne 2003), incubated in a cold room at 0 – 4°C for 1–2 months to overcome dormancy and germinated in a growth room at 18 – 24°C (Ramming 1990; Anderson et al. 2002). Germination at the cooler range will give more consistent germination over a range of genotypes (Anderson et al. 2002). Once the seeds have germinated, the plantlets are transplanted into a sterile soil mix and are slowly acclimated to the low humidity and higher temperature regime of the greenhouse. These are grown in the greenhouse until large enough to transplant to the field.

At the end of the dormant season, seedlings can be transplanted in the orchard at densities ranging from 33,000 (0.3 m × 1 m) to 1,000 (2 m × 5 m) plants per hectare. The higher density approach is possible in low-chilling environments, where long growing season conditions favor rapid tree growth and early fruiting, i.e., from the second season after planting. Owing to this very early selection, seedlings can be pulled out before competition between neighboring trees occurs. The highest density tested so far is the “fruiting nursery” (Sherman et al. 1973) where seedlings are planted 13 cm apart and 1 m between rows. This method proved very effective for breeding goals but not for assessing the genetic nature of many quantitative traits. Lower densities, used in environments featuring short growing seasons or when prolonged life of the trees is envisaged to reduce tree competition, allow normal fruiting and make the choice of the best seedling easier. Also, it is best suited for genetic studies since trees can be grown to their full size.

Selection is usually made in the first good cropping year which varies from the second to the third or fourth year from planting, and from warm to temperate and cold environments, respectively. Usually one year of observation is enough to evaluate most of the progeny, given the phenotypes are a good estimate of the genotype (Hansche et al. 1972) as discussed above.

The evaluation method depends on the goals. When the main goal is market-driven, i.e., the release of a new cultivar, the choice of the best recombinants (seedlings) to be propagated as advanced selections should be mainly based on breeder experience and a sound knowledge of the available commercial cultivars. A common mistake would be to keep (and propagate) too many individuals that do not represent a real improvement toward the present cultivar array. However, some seedlings could be selected if they represent valuable genetic material for further crosses; even if per se they do not bring full commercial value, they will be kept to improve the breeding stock. When selecting for new cultivars, data are taken on only the main traits (bloom and ripening date, flower and leaf traits, fruit type and estimate of the yield potential) of selected seedlings. The others are simply discarded without taking data. In the past, field data were taken manually but considering the large number of seedlings often involved in today’s breeding activity, data are frequently collected directly into a digital format to save time and avoid transcription errors. Nevertheless, paper and pencil can still prove as effective and are more user-friendly in the field under some situations.

When the evaluation of the progeny is focused on genetic investigations more detailed and accurate data should be taken in accordance with the aim of the studied trait(s). For those under simple Mendelian inheritance, data collection is rather trivial, and the data can be evaluated with the chi-square test. For quantitative traits the record keeping is more laborious and the measuring criteria need to be well defined in advance to maximize the usefulness of the data collected. Furthermore, since multi-genic traits are influenced by environmental variability, it is advisable to randomize the seedlings (Okie 1984; Quilot et al. 2004), extend the observations for at least two or even more years and/or plant the population at multiple sites, particularly when linkage studies between QTLs and molecular markers are an objective. When studying the genetic determinants of fruit quality (size, appearance and composition), only a

limited number of fruit per tree should be left to allow for the maximum fruit growth and avoid source competition among fruits (Quilot et al. 2004; Cantín et al. 2009a).

After a seedling has been chosen for further evaluation in a test plot, its sanitary status should be checked to exclude viruses, particularly the *Plum pox virus* (PPV), *Prunus necrotic ring spot virus* (PNRSV), *Prune dwarf virus* (PDV), and other intracellular pathogens (e.g., mycoplasmas) that may hamper yield and/or fruit quality and exclude its introduction into the nursery system. Several diagnostic tests are available, such as ELISA, indicator host plants, and finally, the most sensitive, PCR-based techniques. If the selected seedling is virus-free, some mother trees should then be established in an insect-proof screen house to be kept as the source of clean propagation material for subsequent propagation for testing and possible release.

The advanced selections should be submitted to a testing procedure in comparison with other concurrent selections (e.g., from other breeding programs) and commercially established cultivars according to the ripening season and fruit type. In many breeding programs this is done in collaboration with commercial growers. To this end, trees are grafted on a given rootstock or, better, two or three common rootstocks and in several locations to collect more data prior to the possible release of a new cultivar. While a perfectly sound statistical design with replications is economically impractical in most situations, an experimental design should be planned to collect objective data not biased by the subjective evaluation of the breeder. From a number of studies, plots with a tree number variable from 6 to 8 are enough for yield records and from 15 to 30 fruits per tree are sufficient for quality assessment (Scorza and Sherman 1996). These test plots require at least 2–3 fruiting years of data before a good decision can be made on its commercial potential.

The superior selections from the second testing stage are then entered into the final stage of evaluation, i.e., the growers' acceptance trial. The market success of a putative new cultivar depends mainly on the acceptance of the growers and the retail distribution chain. Frequently, growers in the main fruit growing districts, even from distinct environments, are eager to test promising selections even at no cost for the breeder. At this point the tests are run under a nonpropagation agreement to avoid unintended or illegal propagation of the advanced selections. These final trials, even though performed informally without a statistically sound design, produce much information a breeder has no means to obtain from his formal tests, i.e., the selection's performance under diverse management (tree training and pruning, thinning) and different soils as well as its fruiting and postharvest behavior under a large field harvest operation. An additional 3–5 fruiting years are needed in this final test to raise enough confidence for the introduction of a selection as a new cultivar.

6.4 Release of Cultivars

The creation of a new cultivar is very expensive and a return on the investment is needed, thus legal protection is required. In the past, cultivar protection was sought only by private breeders but today even cultivars from public programs are being

protected. The requirements for protection are different from one country to another. In the USA, patenting a cultivar is equivalent to patenting an industrial process. In the European Union, the Community Plant Variety Office (CPVO) manages a system of plant cultivar rights covering the 27 member states (<http://www.cpvo.europa.eu>). The applicant files an application for protection either directly through the CPVO or through one of the national Plant Breeder's Rights offices that subsequently transfers it to the CPVO. If no obstacle prevents a grant of Community protection, the CPVO takes the necessary measures for organizing the conducting a technical examination of the candidate cultivar. The aim of this is to verify that the cultivar is distinct from others, uniform in its characteristics and stable in the long run (DUS). Once the CPVO considers that the examination results are satisfactory and that all the other requirements have been fulfilled, it grants a Community Plant Variety Right for a period of 30 years for vines, fruit trees, grape, and potatoes. In Europe, a new cultivar receives a certificate that has approximately the same value as a patent in the USA. For a patent to be issued in the USA, a cultivar must be original and healthy (virus free). The legal protection lasts 20 years and covers its phenotype only, fruit included (see Chap. 3 on Intellectual Property).

New peach cultivars have a relatively short market life: 10–20 years at most with a life of a few years not being uncommon. If we compare this duration to what is needed to create a truly innovative cultivar (15–20 years on average), it can be said that this job is not really rewarding. However, some cultivars retain their commercial value for many years, e.g., 'Redhaven' peach worldwide, and now 'Big Top' nectarine in Italy, but they tend to be the exception rather than the rule. The problem lies in the fact that the breeder is often aiming at a moving target. While the new cultivar may have successfully combined the desired characters that were sought when the program was initiated, the cultivar requirements of the market may have changed during the 15–20 year period in which the cultivar was being developed. Thus, the new cultivar may not meet the existing market requirements when released. This is an inherent risk in fruit breeding, but given the genetic advances seen over the last 50 years, it appears to be a risk well worth taking (Monet and Bassi 2008).

It is becoming increasingly common to see new cultivars released after less than 10 years from the original pollination as the nursery industry push for quicker returns from their investment, and growers and their organizations compete for exclusive cultivation rights on new cultivars. This creates a situation in which these are released with minimal testing. This is why tens of newly introduced cultivars are entering the European and USA market every year. The best of these still remain to be identified and proven, often at grower expense.

6.5 Rootstocks

In the last half of the twentieth century, the selection of peach rootstocks was often begun with the identification and collection of spontaneous peach seedlings, wild plums and/or natural peach–almond hybrids, which were incorporated into *Prunus*

collections (Bernhard and Grasselly 1981; Indreias et al. 2004; Moreno 2004). In the first phase, the work basically focused on establishing mother plants and studying their aptitude for sexual or vegetative propagation. For the outstanding clones, their sanitary status was determined and propagation conditions were optimized. In many cases, micropropagation procedures were established, which also accelerated the breeding process by allowing the rapid clonal propagation of *Prunus* hybrids from controlled interspecific crosses to produce plants for evaluation.

To assess scion-rootstock compatibility, experimental nurseries are established to ascertain good graft compatibility of the new rootstocks, mainly when species from botanical sections different from *Euamygdalus* are used. Cases of “translocated” incompatibility in peach are usually expressed during the first year of scion growth, but the occurrence of the “localized” cases may be delayed, and subsequently, more years are necessary to evaluate this feature (Zarrouk et al. 2006). To determine the influence of the outstanding clones on the productive characteristics of peach cultivars (e.g., vigor, yield, and fruit quality), orchard trials are established to assess their performance in the most important areas of production, including a range of soils and pathological challenges. During the last half of the twentieth century, this selection process usually took 20–40 years before a new peach rootstock could be released and widely used into the peach industry.

Traditional selection procedures used to detect tolerance to abiotic stresses (iron chlorosis and waterlogging) are based on field evaluation and usually requires several years. Therefore, new evaluation methods using hydroponic culture have been also developed to select new genotypes tolerant to iron chlorosis based on the root capacity to reduce Fe-chelates (Cinelli and Loreti 2004; Jiménez et al. 2008). Similarly, evaluation for tolerance to waterlogging have been also conducted in specially designed tanks where the soil is flooded and selection is based on the rate at which plants develop symptoms of waterlogging and root asphyxia (Salesses et al. 1970; Amador et al. 2010). In the case of nematodes, tests are usually carried out with plants growing in infected pots established in greenhouses. With these procedures, rootstock evaluation to these stresses can be carried out in several months (Pinochet et al. 1999; 2002).

6.6 Propagation

Peach seedling rootstocks have been primarily used in the world because of the availability of inexpensive seeds, the ease of sexual propagation and the good compatibility with budded peach cultivars. However, the horticultural advantages of peach–almond hybrids and plum rootstocks for peaches led to the development of new methods of vegetative propagation. Hardwood and softwood cutting propagation were first established by defining the most appropriate auxins (type and concentration) and timing of propagation during the year (Howard 1987; Webster 1995). At present, all these methods are being replaced by tissue culture of clonally micropropagated selections to produce thousands or millions of plants annually

(Battistini and De Paoli 2002), although micropropagated rootstocks frequently sucker more profusely than those from conventional cutting techniques (Webster 1995). This technique also has value in facilitating the movement of healthy materials over national borders while satisfying plant importation and health regulations. These successful propagation techniques developed for *Prunus* clonal rootstocks and interspecific hybrids has further accelerated interest and research into molecular genetics and MAS in peach rootstocks (Lu et al. 2000; Dirlewanger et al. 2004a).

7 Integration of New Biotechnology in Breeding Programs

7.1 Molecular Markers

Molecular markers have been used in peach for genotyping and genetic diversity analysis (Dirlewanger et al. 2002; Aranzana et al. 2003a; Riaz et al. 2004; Yoon et al. 2006; Bouhadida et al. 2007a, b, 2009, 2011), development of linkage maps (Chaparro et al. 1994; Rajapakse et al. 1995; Dirlewanger et al. 1998; Yamamoto et al. 2001; 2005), trait tagging and MAS (Foulongne et al. 2002; Lecouls et al. 2004; Blenda et al. 2007), and for quantitative trait loci (QTL) positioning (Dirlewanger et al. 1999, 2006; Quilot et al. 2004; Cantín et al. 2010b). A number of molecular marker systems, such as isoenzymes, restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), fragment length polymorphism (AFLP), and simple sequence repeats (SSRs) have been used in peach for the identification of markers tightly linked to traits of interest (Chaparro et al. 1994; Sosinski et al. 1998; Quarta et al. 1998; Joobeur et al. 1998; Dirlewanger et al. 1998; Dettori et al. 2001; Verde et al. 2005). Owing to their abundance, high polymorphism, codominance, reproducibility, and transferability to related species, SSRs are emerging as a marker of choice for linkage and comparative mapping, genotype identification, QTL tagging, and MAS (Cipriani et al. 1999; Aranzana et al. 2002; 2003a, b; Dirlewanger et al. 2004b; Liu et al. 2007). Moreover, the large expansion of DNA databases, particularly those containing EST sequences, has now opened the opportunity for the identification of single nucleotide polymorphisms or (SNPs) in peach (Lazzari et al. 2008). Typically, however, RFLP, RAPD, AFLP, and SSR markers are only genetically linked to the trait of interest, and no functional relationship can be inferred. Therefore, a candidate gene/QTL approach is necessary to associate major genes and QTLs involved in expression of traits of interest to structural genes in peach.

7.2 State of the Map

Chaparro et al. (1994) developed the first genetic map for peach using molecular markers. Since then, nine linkage maps have been constructed for peach (Dirlewanger and Bodo 1994; Dirlewanger et al. 1998; Rajapakse et al. 1995; Abbott et al. 1998),

and six interspecific maps between peach and other members of the genus *Prunus*, namely, peach \times almond (Joobeur et al. 1998; Foolad et al. 1995; Jáuregui et al. 2001), peach \times *P. davidiana* (Dirlewanger et al. 1996), peach \times *P. ferganensis* (Quarta et al. 1998), and myrobalan plum \times (almond \times peach hybrid) (Dirlewanger et al. 2004a), have been constructed (Table 14.4).

The ‘Texas’ (almond) \times ‘Earlygold’ (peach) linkage map (T \times E) is the first saturated linkage map constructed completely from transferable markers and is considered the reference map for *Prunus* L. (Joobeur et al. 1998; Dirlewanger et al. 2004a) (<http://www.bioinfo.wsu.edu/gdr/>). In addition to 826 markers currently placed on the T \times E map (Dirlewanger et al. 2004b; Howad et al. 2005), Abbott et al. (2007) recently reported on mapping efforts that tentatively put an additional 600 EST sequences on this map. The existence of the T \times E map has been very useful for the *Prunus* research community, providing a highly polymorphic population for linkage studies, establishing a common terminology for linkage groups, and providing a set of transferable markers (“anchor” markers) of known map position that facilitated the development of framework maps in other crosses. It also allowed the location of different major genes and QTLs in a unique map, the search for markers to saturate specific genomic regions, and the establishment of map comparisons with other *Prunus* species (Dirlewanger et al. 2004b).

7.3 Traits Tagged with Molecular Markers

Peach has a relatively small genome, estimated at 300 Mb in the haploid genome (Arumuganathan and Earle 1991; Baird et al. 1994), and is considered genetically the best characterized species in *Prunus* and among fruit trees (Mowrey et al. 1990). There are 43 morphological characters with simple Mendelian inheritance in peach (Dirlewanger et al. 2004b; Dirlewanger and Arús 2005) and for 23 of them linkage relationships with molecular markers have been determined (Table 14.5). So far, molecular markers are proposed for only 20 peach monogenic traits, and only for 12 of those the linkages are tight enough (less than 5 cM) to be sufficient for MAS (Table 14.5).

Molecular markers linked to six Mendelian characters have recently been reported (Dirlewanger et al. 2006): pollen sterility, peach or nectarine fruit, saucer or round fruit, clingstone or freestone fruit, low acidity in fruit, and fruit abortion. The character of trees bearing aborting fruit (*Af*) is recessive and linked to the saucer gene, and is bounded by two SSR markers, MA040a and MA014a. For the other five traits, linkage relationships were previously reported and placed on the *Prunus* reference map (Dirlewanger et al. 2004b), but tightly linked PCR based molecular markers were lacking. Although peach genomic and EST sequence databases are constantly expanding and a highly saturated *Prunus* reference map is available, there is still a need for markers, preferably PCR based ones such as SSRs, which are tightly linked to loci of agronomic importance. Wang et al. (2002b) identified SSR loci tightly linked to two important peach traits, root-knot nematode resistance and

Table 14.4 Peach intra- and interspecific linkage maps

Population	Type	Marker #	LG #	Map size (cM)	References
<i>P. persica</i> × <i>P. persica</i>					
Weeping clone (1161:12 × 2678:47) 1:55 × 'Early Summergrand'	F ₂	52	8	350	Dirlewanger and Bodo (1994)
NC174RL × 'Pillar'	F ₂	88	15	396	Chaparro et al. (1994)
'New Jersey Pillar' × 'KV77119'	F ₂	58	13	540	Rajapakse et al. (1995); Abbott et al. (1998); Sosinski et al. (2000)
'Suncrest' × 'Bailey'	F ₂	147	23	926	Abbott et al. (1998); Sosinski et al. (2000)
'Lovell' × 'Nemared'	F ₂	153	15	1,300	Abbott et al. (1998); Lu et al. (1998); Sosinski et al. (2000)
'Harrow Blood' × 'Okinawa'	F ₂	76	10		Gillen and Bliss 2005
'Akame' × 'Juseitou'	F ₂	178	8	571	Shimada et al. (2000); Yamamoto et al. (2001, 2005)
'Ferjalou Jalousia' × 'Fantasia'	F ₂	181	7	621	Dirlewanger et al. (1998, 2006); Etienne et al. (2002)
'Contender × Fla.92-2C'	F ₂	127	8	535	Fan et al. 2010
'Guardian [®] ' × 'Nemaguard' (<i>P. persica</i> × <i>P. davidiana</i>)	F ₂	158	11	737	Blenda et al. (2007)
<i>P. dulcis</i> × <i>P. persica</i>					
'Texas' × 'Earlygold'	F ₂	826	8	524	Joobeur et al. (1998); Aranzana et al. (2003b); Dirlewanger et al. (2004b); Howad et al. (2005)
'Padre' × '54P455'	F ₂	161	8	1,144	Foolad et al. (1995); Bliss et al. (2002)
'Garfi' × 'Nemared'	F ₂	51	7 ^a	438	Jáuregui et al. (2001)
<i>P. persica</i> × <i>P. ferganensis</i>					
IF7310828 ('J.H. Hale' × 'Bonanza') × <i>P. ferganensis</i>	BC ₁	216	8	665	Quarta et al. (1998, 2000); Verde et al. (2005)
<i>P. persica</i> × <i>P. davidiana</i>					
'Summergrand' × Clone P1908	F ₁	23/97 ^b	3/9	159/471	Dirlewanger et al. (1996); Viruel et al. (1998); Foulongne et al. (2002)
'Rubira × Clone P1908'	F ₁	4/88 ^b	0/8	454.2	Rubio et al. (2010)
<i>(P. cerasifera)</i> × (<i>P. dulcis</i> × <i>P. persica</i>)					
P.2175 × GN22 ('Garfi' × 'Nemared')	F ₁	93/166 ^b	8/7	525/716	Dirlewanger et al. (2004a)

^aLinkage groups 6 and 8 of this map were mapped as a single group due to a reciprocal translocation

^bSeparate maps were created for each parent

Table 14.5 Molecular markers linked to monogenic traits in peach

Trait	Gene	Marker name	Distance ^a (cM)	Reference
<i>Flower</i>				
Double flower	<i>Dl</i>	<i>pchgms1</i>	7.8	Sosinski et al. (2000)
Flower color	<i>Fc</i>	<i>EACA/MCTG-220</i>	7.1	Yamamoto et al. (2001)
Male sterility	<i>Ps</i>	<i>FG40</i>	4.8	Dirlewanger et al. (2006)
<i>Leaf</i>				
Leaf color	<i>Gr</i>	<i>UDP96-015</i>	3.7	Yamamoto et al. (2001)
Leaf glands	<i>E</i>	<i>AG104</i>	2	Dettori et al. (2001)
Leaf shape	<i>Nl</i>	<i>EAC/MCAC-180</i>	12.0	Yamamoto et al. (2001)
<i>Tree</i>				
Dwarf plant	<i>Dw</i>	<i>EAC/MCAC-180</i>	12.0	Yamamoto et al. (2001)
Pillar growth habit	<i>Br</i>	<i>pchgms1</i>	12.5	Sosinski et al. (2000)
Evergrowing	<i>evg</i>	<i>EAT/MCAC</i>	1.0	Wang et al. (2002b)
		<i>pchgms10</i>	1.0	
		<i>pchgms11</i>	1.0	
		<i>pchgms12</i>	1.0	
		<i>pchgms13</i>	1.0	
		<i>pchgms14</i>	1.0	
<i>Fruit</i>				
Blood flesh	<i>bf</i>	<i>C41H</i>	10.3	Gillen and Bliss 2005
Saucer fruit	<i>S</i>	<i>MA040a</i>	0	Dirlewanger et al. (2006)
Aborting fruit	<i>Af</i>	<i>MA040a</i>	0	Dirlewanger et al. (2006)
Flesh adhesion	<i>F</i>	<i>UDAp-431/b</i>	1.2	Dirlewanger et al. (2006)
		<i>BPPCT009/b</i>	2.2	
		<i>AG12 & AG16b</i>	2.0	
Flesh color	<i>Y</i>	<i>UDP98-407</i>	2.2	Mingliang et al. 2007
Flesh color around stone	<i>Cs</i>	<i>OPO2/0.6</i>	12.4	Yamamoto et al. (2001)
Nonacid fruit	<i>D</i>	<i>pTC-CTG/a</i>	0	Dirlewanger et al. (2006)
		<i>pGT-TTG/a</i>	0	
Skin color	<i>Sc</i>	<i>UDP96-015</i>	3.7	Yamamoto et al. (2001)
Skin pubescence	<i>G</i>	<i>eAC-CAA/a</i>	0	Dirlewanger et al. (2006)
		<i>UDP96-018</i>	4.5	
<i>Pest resistance</i>				
Nematode resistance	<i>Mij</i>	<i>EAA/MCAT10</i>	3.4	Lu et al. (1998)
		<i>pchgms26</i>	3.4	Wang et al. (2002a)
		<i>ISSR834-1/0.4</i>	4.8	Wang et al. (2002a)
		<i>Mja</i>	<i>EAA/MCAC-135</i>	4.8

^acM distance <5 is considered close enough for MAS

evergrowing, by using the high-throughput technique of AFLP mapping with subsequent direct targeting of SSRs identified in AFLP-marked regions of interest. However, this approach relies on the availability of a peach bacterial artificial chromosome (BAC) library resource. Examples of using bulk segregant analysis (BSA) in discovering markers tightly linked to disease resistance traits are also available in peach (Claverie et al. 2004a, b; Lecouls et al. 2004; Gillen and Bliss 2005).

Most agronomically important traits in which breeders are interested exhibit continuous phenotypic variation indicating more complex, polygenic control. There are 25 peach traits associated with QTLs, and most of them are related to fruit quality (Abbott et al. 1998; Dirlewanger et al. 1999; Quarta, et al. 2000; Etienne et al. 2002; Peace et al. 2006; Cantín et al. 2010b), adaptation (Abbott et al. 1998; Dirlewanger et al. 1999; Quarta et al. 2000; Etienne et al. 2002; Blenda et al. 2007) or disease resistance (Dirlewanger et al. 1996; Viruel et al. 1998). The detection of QTLs related with tolerance to abiotic stresses as iron chlorosis, and the search of candidate genes differentially expressed under iron deficiency is under development. Preliminary results have showed QTLs located in chromosomes 6 and 8 (Gonzalo et al. 2009), near other QTLs involved in fruit quality and nematodes resistance (Yamamoto et al. 2001; Dirlewanger et al. 2004a). The candidate genes approach has been implemented based on *in silico* screening of genes shown to be expressed in response to iron deficiency in roots (Gonzalo et al. 2011).

High level of synteny and colinearity between different *Prunus* maps and the existence of a reference map for the genus allowed integration of 28 major *Prunus* genes, mapped in populations of apricot, peach, almond, and myrobalan plum, into a single map (Dirlewanger et al. 2004b). The approximate position of these genes on the T×E map and information available from the interconnecting *Prunus* maps allows the discovery of additional markers in regions of interest and their usage in MAS.

7.4 *Marker-Assisted Selection*

Peach breeding has been very active in the last decade with hundreds of new cultivars released (Sansavini et al. 2006). The ability of breeders to generate large populations is almost unlimited, but the management, phenotyping and selection of these seedlings are the main limiting factors for the generation of new cultivars. Molecular markers linked to traits of interest are essential for both MAS and improvement of selection efficiency in standard breeding procedures, especially for economic traits that are difficult to select by phenotype early in the plant life cycle. MAS is particularly useful when the expression of the gene is recessive and the evaluation of the character is expensive or time-consuming or, in tree crops such as peach, with long juvenile periods (Scorza 2001; Luby and Shaw 2001). The low level of variation found in peach (Byrne 1990) and the narrow genetic base of modern peach cultivars (Scorza et al. 1985) impede implementation of MAS in peach breeding programs. One of the major impediments to using MAS in applied breeding of fruit crops identified by breeders in a survey was the lack of markers and simplified technology to screen progenies (Byrne 2007). These impediments are being addressed in several large collaborative research programs in both Europe (Audergon et al. 2009; Dirlewanger et al. 2009) and the USA (Iezzoni et al. 2009).

MAS is currently used in rootstock breeding programs for early selection for resistance genes to root-knot nematode (*Meloidogyne* spp.) from two sources: peach (Lu et al. 1998; Yamamoto and Hayashi 2002; Arús et al. 2004) and myrobalan

plum (Lecouls et al. 1999, 2004; Claverie et al. 2004a, b). In addition, Claverie et al. (2004a, b) showed that plum and peach genes are nonallelic and thus can be pyramided into interspecific hybrid rootstocks based on the plum and peach species. Recently, another successful implementation of MAS has been reported for the recessive character *Af* that encodes the fruit abortion trait in peach trees (Dirlewanger et al. 2006). Despite the growing availability of genomic resources in peach, the existence of a highly saturated reference T × E map [826 markers with average density of 0.63 cM per marker, Dirlewanger et al. (2004a, b, c) and Howad et al. (2005)] and most of the simple characters being sufficiently marked for selection (Table 14.5), the use of markers for commercial breeding in peach is still in its infancy. In addition, most of the agronomic important traits are quantitatively inherited and although 28 QTL have been identified in *Prunus*, further work is necessary before QTL-associated markers can routinely be integrated into selection programs.

7.5 Genomics

The availability of whole genome sequences and expressed sequence tag (EST) databases for important crops is accelerating the process of gene discovery. The recently released first draft of the assembled peach genome sequence, *peach v1.0* (<http://www.rosaceae.org/peach/genome>), along with previously available *Prunus* Genome (<http://www.rosaceae.org/>) and ESTree databases (<http://www.itb.cnr.it/estree/index.php>), provides access to genomic data for peach and constitutes very useful sources of information for genome comparative studies and identification of important genes. Abbott et al. (2002) first reported on the initiative to build genomic resources using peach as a model for the identification, characterization, and cloning of important genes of Rosaceae species. Since then, several BAC libraries have been constructed for peach (<http://www.bioinfo.wsu.edu/gdr/>) (Wang et al. 2001; Georgi et al. 2002; Boudehri et al. 2009). The BAC library constructed from fruit mesocarp of the peach rootstock ‘Nemared,’ consisting of 44,160 clones with an average size of 70 kb and 8.8-fold genome coverage (Georgi et al. 2002), and the BAC library from a haploid of the peach rootstock “Lovell” with 34,560 clones having an average insert of 80 kb providing 9.2-fold genome coverage (L. Georgi, unpublished data), have been used for the development of a framework physical map for peach (Zhebentyayeva et al. 2008). Two hundred and fifty-two clones, out of 2,138 contigs that form the initial physical map of peach, were anchored to eight linkage groups of the *Prunus* reference map.

Approximately 100,000 EST sequences from different *Prunus* species have been sequenced and deposited to NCBI and ESTree databases (<http://www.ncbi.nlm.nih.gov>; <http://www.itb.cnr.it/estree/index.php>). Most of the *Prunus* ESTs originated from 19 peach libraries, representing nine cultivars and four tissues from four developmental stages (Lazzari et al. 2005). Peach EST-SSRs, originated from fruit transcriptome, have already been isolated and show transportability across other *Prunus* species (Vendramin et al. 2007) and/or were tentatively mapped to the *Prunus* reference map (Abbott et al. 2007). Additionally, development of a peach transcript

map (Horn et al. 2005; Abbott et al. 2007) and its integration with the physical map (Zhebentyayeva et al. 2008) was reported. This provides the necessary foundation for the identification of candidate genes that control many important fruit tree characters.

Breeding for disease resistance is a major goal in most cultivar development programs. The identification of loci for pathogen resistance in peach would provide information about resistance loci, the organization of resistance genes throughout the genome, and permit comparison of resistance regions among other genomes in the Rosaceae. Lalli et al. (2005) generated a resistance map for *Prunus* using a candidate gene approach. Resistance gene analogs (RGAs) and resistance-associated genes (RAGs) were hybridized to a peach BAC library and mapped using the peach physical map database and the Genome Database for Rosaceae (GDR). More than 40 RGAs and RAGs are mapped in regions known to contain resistance to powdery mildew, plum pox virus, and parasitic nematodes (Lalli et al. 2005; Abbott et al. 2007).

7.6 Transgenics

Improvement of fruit tree species through traditional breeding methods is a long-term effort due to their lengthy juvenile periods. Genetic transformation presents a promising tool for genetic improvement of peach and other woody fruit species. The main obstacle to genetic engineering of fruit tree species is the regeneration of transformed tissues/plantlets. Therefore, to use genetic engineering techniques for germplasm improvement, reliable protocols for transformation, selection, and regeneration of transgenic plantlets are needed. There are several reports of using different peach explants for regeneration: immature zygotic embryos (Hammerschlag et al. 1985; Hammerschlag 1988), immature cotyledons (Mante et al. 1989), embryo cells (Smigocki and Hammerschlag 1991), mature cotyledons (Pooler and Scorza 1995), and recently, mature embryos (Pérez-Clemente et al. 2005) and in vitro leaf tissue (Gentile et al. 2002).

Most of the work on peach transformation was done using *Agrobacterium*-mediated transformation. However, gene delivery via particle bombardment to embryonic callus derived from immature embryos has also been reported (Ye et al. 1994). Although high levels of transformation were demonstrated, no regeneration was obtained from the transformed embryogenic callus. In spite of much work and dedication, peach regeneration remains difficult; for example, only two reports of stable peach plant transformants have been published, and a total of four transgenic plants have been produced (Smigocki and Hammerschlag 1991; Pérez-Clemente et al. 2005). In addition, successful transformation and in vitro regeneration of peach plants was reported mostly from zygotic tissue, which is not favored for fruit tree transformation because the ability to improve established cultivars is lost (Abbott et al. 2007). However, while *Prunus* breeders and geneticists wait for efficient and repeatable transformation methodology for peach somatic tissues, breeding programs are now using and benefiting from current technologies such as MAS to incorporate targeted genes into elite germplasm.

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