Chapter 9
Peaches

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Abstract Common goals of peach breeders are: (1) extending the harvest season, (2) improving flavor and aroma, (3) lengthening self life, (4) controlling tree size, (5) broadening the adaptive range, and (6) developing resistance to sharka (PPV), powdery mildew, brown rot, leaf curl, *Xanthomonas* spp. and the green aphid (the vector of PPV). A number of single genes have been identified that reduce tree size and modify plant shape, and regulate firmness, mealiness, melting flesh, browning, flesh color and the freestone trait. Fruit maturity has been shown to be quantitatively regulated with a very high heritability. A growing number of molecular linkage maps have been developed of peach and its relatives; map coverage ranges from 396 to 1300 cM, with 8 to 23 linkage groups being identified. QTL have been identified for numerous horticulturally important traits including bloom and ripening time, fruit quality, storage life, freestone trait, internode length and pest resistance. Several bacterial artificial chromosome (BAC) libraries have been developed for peach and over 85,000 *Prunus* ESTs have been sequenced and deposited in the NCBI dbEST database. Peaches have been regenerated utilizing several systems, but there are only two reports of stable peach plant transformation.

9.1 Introduction

The peach, and its smooth skinned mutant, the nectarine, are primarily grown in temperate zones, between latitudes 30 and 45 N and S. The peach flower bud is hardy to about -23° C to -26° C which limits its cultivation at higher latitudes. Most peach cultivars require from 100–1000 hours of chilling below 7° C and they are highly susceptible to early spring frosts.

The fruits of peach cultivars vary widely across the world and even within regions. Fruit shapes vary from beaked, round to flat, colors vary from yellow, white to red, the flesh can be melting or non-melting and they can be clingstone or freestone.

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Peaches are eaten fresh, canned or dried and are excellent sources of fiber, vitamins and antioxidants (http://riley.nal.usda.gov/NDL/cgi-bin/list_nut_edit.pl). The highest quality peaches are produced in regions with warm to hot summers.

Worldwide production of peaches is now in excess of 15,000,000 tonnes, with almost half of the production coming from Asia (mostly China) (Sansavini et al. 2006). Among the deciduous fruits, peaches rank second to only apples in tonnage. Europe accounts for about 30% of the peach crop, while North America contributes 11%, South America 6% and Africa 5%. The major producers in Europe are Italy, Greece and Spain; in North America the greatest concentration of production is found on the western and eastern seaboards, and along the Great Lakes. The peach industry in Asia has grown dramatically over the last decade, while peach production in the rest of the world has shown only moderate to little change. The peach industry in South America is still limited, but increasing in Chile and Brazil.

9.2 Evolutionary Biology and Germplasm Resources

The peach [*Prunus persica* (L.) Batsch] is the most widely grown species in a very important genus containing the European plum (*P. domestica* L.), Japanese plum (*P. salicina* Lindl.), apricot [*P. armeniaca* (L.) Kostina], almond (*P. amygdalus* Batsch), sweet cherry (*P. avium* L.), and sour cherry (*P. cerasus* L.). Peach belongs to the family Rosaceae and the subgenus *Amygdalus*. Unusual in its subgenus, the peach is largely self fertile. There are at least 77 wild species of *Prunus* and most of them are found in central Asia. While polyploidy is common in the genus *Prunus*, the cultivated peach is diploid and has a chromosome number of $2n = 2x = 16$.

Five species that can be termed 'peach' are generally recognized: *P. persica*, *P. davidiana* (Carr.) Franch, *P. mira* Koehne, *P. kansuensis* Rehd. and *P. ferganensis* (Kost. & Rjab) Kov. & Kost. All are found in China (Table 9.1). The domesticated

Table 9.1 Native peach species

Species	Common name	Chromosome number ($2n$)	Distribution
P. davidiana (Carr.) Franch	Mountain peach, Shan tao	16	N. China
P. ferganensis (Kost. & Rjab) Kov. & Kost.	Xinjiang tao	16	N.E. China
P. kansuensis Rehd.	Wild peach, Kansu tao	16	N.W. China
P. mira Koehne	Tibetan peach, Xizang-tao	16	W. China & Himalayas
P. persica (L.) Batsch	Peach, Maotao	16	China

Adapted from Scorza and Okie 1990

Table 9.2 *Prunus* species that have been hybridized with *P. persica* that form mostly sterile hybrids

Species	Common name	Origin
P. americana Marsh.	American plum	U.S.A.
P. armeniaca L.	Apricot	Asia
P. besseyi Bailey	Western sand cherry	N. U.S.A., Canada
P. brigantine Vill.	Briancon apricot	France
P. cerasifera Ehrh.	Myrobolan plum	W. Asia
P. cerasus L.	Sour Cherry	W. Asia, S.E. Europe
P. domestica L.	European plum	W. Asia, Europe
P. hortulana Bailey	Wild plum	Central U.S.A.
P. japonica Thunb	Chinese or Korean bush cherry	China
P. munsoniana Wight & Hedr.	Wild goose plum	Central U.S.A.
P. nigra Ait	Canadian plum	N. U.S.A., Canada
P. pumila L.	Eastern sandcherry	N. U.S.A.
P. salicina Lindl.	Japanese plum	China
P. simmonii Carr.	Simon's plum	N. China
P. spinosa L.	Sloe	Europe, W. Asia, N. Africa
P. tenella (=*nana*) Batsch	Siberian almond	S.E. Europe, W. Asia
P. tomentosa Thumb.	Chinese bush cherry	N. & W. China, Japan
P. virginiana L.	Choke cherry	N. U.S.A., Canada

Adapted from Scorza and Okie 1991

peach can be readily hybridized with native populations of *P. persica* and all the other wild species of peach. Successful hybrids have also been produced between peach and almond, apricot, plum and sour cherry (Table 9.2). In most cases, these wide hybrids are largely sterile, although F_1s of almond and peach can be highly fertile (Armstrong 1957) and can be employed as rootstocks for both peach and almond.

9.3 History of Improvement

Peach cultivation probably originated in western China from wild populations of *P. persica* (Hedrick 1917, Scorza and Okie 1991). The peach is mentioned in 4,000 year old Chinese writings, and most of the known variation in cultivated peaches is found in Chinese land races. Peaches arrived in Greece through Persia about 2,500 B. P. and in Rome 500 years later. The Romans spread the peach throughout their empire. The peach came to Florida, Mexico and South America in the mid 1500s via Spanish and Portuguese explorers. It became feral in the southeastern United States and Mexico, and was further spread throughout North America by the Native Americans.

A rapid expansion in fruit culture arose in Europe during the Industrial Revolution of the 16th century, as a growing class of people acquired substantial wealth and began to garden. Numerous cultivars were released during this period by active fruit tree breeders such as John Rivers. Many of these cultivars

were released as clones, although many may also have been distributed from seed. Peach breeding began about 100 years ago in the North American colonies, utilizing two major sources of germplasm – naturalized seedlings from the southeastern U.S.A. and Mexico, and cultivars originated in England. Until the American Revolution, peaches were mostly produced in seedling stands of very low quality. The first budded trees were offered for sale by Robert Prince on Long Island just before the Revolutionary War and by John Kenrick of Massachusetts in the 1790s (Hedrick 1950).

A number of cultivars of unknown origin were released in the first half of the 1800s including 'Early Crawford', 'Late Crawford' and 'Oldmixon Cling'. In 1850, Charles Downing introduced 'Chinese Cling' from China to the United States via England, and it was originally planted in South Carolina by Henry Lyons (Scorza and Sherman 1996). After the Civil War, Samuel Rumph planted 'Chinese Cling' in Marshallville, Georgia and released two important cultivars from that field, 'Belle of Georgia' ('Belle') and 'Elberta', which likely had 'Chinese Cling' as a parent. Other important, early cultivars were 'Hiley' (a seedling of 'Belle') and 'J.H. Hale' (a seedling of 'Elberta'). This small group of cultivars formed the foundation of most subsequent breeding activity (Scorza et al. 1985). Cullinan (1937) has provided a list of the most significant cultivars that were released between 1850 and 1900.

Peach breeding began in earnest at a number of State Experiment Stations in the late 1890s and early 1900s. Among the earliest large programs were in California, New Jersey and the United States Department of Agriculture. Stanley Johnston in Michigan began his landmark program in 1924 and developed the 'Redhaven' peach, which dominated peach cultivation in the eastern U.S.A. for decades (Iezzoni 1987). Other early, large public programs in the U.S.A. were at Arkansas, North Carolina, Louisiana, Texas, Florida and South Carolina (Childers and Sherman 1988, Cullinan 1937, Okie et al. 1985). Vineland in Canada has had a breeding program since 1914, along with Harrow since 1960. Significant peach breeding efforts have also been undertaken in Argentina, Australia, Brazil, China, France, Italy, Japan, Mexico and South Africa (Childers and Sherman 1988, Li 1984, Okie et al. 1985, Wang and Lu 1992, Yoshida 1988). In the middle of the century, several major private breeding efforts emerged in the US including Grant Merrill, F. W. Anderson and Armstrong Nursery Company. More recent public companies are Zaiger Genetics, Metzler and Sons, Bradford and Bradford, Paul Friday, and Fruit Acres (A. and R. Bjorge).

9.4 Current Breeding Efforts

Worldwide breeding activity has been very high over the last decade, with likely over a thousand new varieties being released. Sansavini et al. (2006) has called the 20th century, the 'Golden Age of Peach Breeding'. The private sector is responsible

for most of the new peach releases, although the new non-melting flesh clingstone varieties for canning have come from the public sector. Over half of the releases (55%) have come from the U.S.A. and 30% from Europe, with France and Italy leading the way (Table 9.3). Most of the cultivar releases are yellow-fleshed peaches and nectarines, although a number of white fleshed cultivars have been developed in France, China, Japan and South Korea.

Among the most important advances are 'a notable enhancement of such fruit quality traits as increased fruit size, fuller and more extensive blush, better skin ground color, increased flesh-to-pit ratio, etc.' (Sansavini et al. 2006). The harvest calendar has been dramatically increased from two-three months to four-six months, and chilling requirements have been substantially lowered to allow expansion into more subtropical climates.

There are a number of traits that are being targeted by breeders as high priorities. Expanding the environmental ranges of peach is a common goal, in some cases to reduce chilling requirements to further expand into the subtropical climates of Spain, France, Italy, U.S.A. and China, but also to increase frost tolerance through

Table 9.3 Peach and nectarines released worldwide by country 1999–2001

Region	Peach		Nectarine		Clingstone		Total
	Yellow	White	Yellow	White	Yellow	White	
Africa							
Egypt	0	3	0	0	0	0	3
South Africa	7	1	8	0	5	0	21
Asia							
China	4	29	11	10	2	1	57
Japan	7	30	0	0	3	0	40
South Korea	1	10	2	0	0	0	13
Taiwan	1	0	0	0	0	0	1
Europe							
Czech Republic	8	0	1	0	0	0	9
France	35	42	24	33	6	0	140
Italy	51	32	37	14	3	4	141
Moldavia	7	0	0	0	0	0	7
Poland	2	0	0	0	0	0	2
Romania	4	0	6	0	0	0	10
Spain	6	3	7	2	3	1	22
Ukraine	10	0	1	0	5	0	16
Oceana							
Australia	1	1	2	0	8	0	12
North Zealand	1	7	0	1	0	0	9
North America							
Canada	2	0	1	0	4	0	7
Mexico	0	0	0	0	18	0	18
U.S.A.	219	107	160	77	21	0	584
South America							
Brazil	0	3	3	1	5	0	12

Source: Sansavini et al. 2006

bloom delay in the colder climates of Canada, Poland and Russia. Considerable effort is also being undertaken to develop a broad range of very early and late ripening types to expand production windows. Strong efforts are being made to increase fruit quality by enhancing appearance, along with improved flavor and aroma. Many European programs are committed to recovering the sensory traits of old cultivars, and Chinese programs are particularly interested in low-acid types (Sansavani et al., 2006). Improving self life by developing firmer fruit is also an important goal of most programs, with the added benefit of reduced damage during handling. The reduction of postharvest disorders related to long-distance shipping of peaches, especially between the northern and southern hemispheres, is an important goal for programs in countries such as Chile, South Africa, New Zealand, and the U.S.A. Control of tree size and vigor is an important goal of most programs, to facilitate mechanization and reduce the costs of pruning, thinning and harvesting (Scorza et al. 2000).

The most widespread disease and pest problems that are being pursued are sharka (PPV), powdery mildew, brown rot, leaf curl, *Xanthomonas* spp. and green aphid (the vector of PPV). Other significant breeding efforts are focusing on nematode (China and the U.S.A.) and phytoplasma resistance (Romania).

Rootstock breeding also remains a high priority at many locations, with most of the research being targeted towards tree vigor management, ease of clonal propagation, soil adaptability (drought and lime), nematode resistance and resistance to bacterial and virus diseases (*Xanthomonas*, *Pseudomonas*, PPV and ACLR) (Layne 1987).

Peach breeding world-wide is a productive endeavor that supplies a large number of improved cultivars each year allowing growers an ample choice of material ripening over a long season, filling a wide range of ecological conditions and satisfying a range of consumer demands. Nevertheless, there are serious needs that remain to be addressed and these needs will become more critical with time. The critical issues that can be at least partially if not fully addressed through breeding include climactic change which may significantly alter biotic and abiotic stress factors, global marketing of fruits increasing competition between peach growing regions and between peach and a vast array of other fruits, and the changing eating habits of populations, especially in developed countries, with emphasis on nutrition and convenience. To meet these challenges will require an even greater commitment to peach breeding that will include exploration of new germplasm, and the application of complementary genomic breeding technologies such as molecular marker assisted breeding and genetic engineering. The development and application of these technologies for the production of new cultivars with improved quality, nutrition, pest and abiotic stress resistance, and market novelty will require additional resources supplied over extended periods of time. Intra and inter institutional collaborations will be necessary in order to utilize diverse genetic improvement technologies. Training the next generation of breeders and the development of fruit improvement teams that span laboratory and field will play critical roles in the continued success of peach as an important crop that sustains grower investment and adds to the health and well being of consumers.

9.5 Genetics of Economically Important Traits

9.5.1 Pest and Disease Resistance

Some of the most widespread disease problems that concern peach breeders are bacterial canker (*Pseudomonas syringae*), bacterial spot (*Xanthmonas campestris*), brown rot (*Monilinia fruticola*), fungal gummosis (*Botrysphaeria dothidea*), leaf curl (*Taphrina deformans*), Leucostoma (Cytospora), canker (*Leucostoma persoonii*), powdery mildew (*Sphaerotheca pannosa*) and sharka (PPV) (Table 9.4). Among the most important pests receiving breeder attention are peach tree borers (*Synanthedon exitiosa*) and the green aphid (*Myzus persicae*) which is a vector of PPV.

Table 9.4 Genetics of disease resistance in peach

Disease	Observations and source
Bacterial	
Bacterial canker *Pseudomonas syringae*	Most cultivars are susceptible; but sources of resistance exist (Gardan et al. 1971, Weaver et al. 1979)
Bacterial spot *Xanthomonas campestris*	Dominant genes may regulate resistance (Sherman and Lyrene 1981); highly resistant cultivars identified (Keil and Fogle 1974, Simeone 1985, Werner et al. 1986)
Fungi	
Brown rot *Monilinia fructicola*	Little resistance in most cultivars, but sources of resistance may exist (Scorza and Okie 1991, Feliciano et al. 1987)
Cytospora canker *Leucotoma persoonii*	Little resistance in most cultivars, but sources of resistance exist (Gairola and Powell 1970, Hampson and Sinclair 1973, Scorza and Pusey 1984)
Fungal gummosis *Botryosphaeria dothidea*	Most cultivars are susceptible, but sources of resistance exist (Daniell and Chandler 1982, Okie and Reilly 1983)
Leaf curl *Taphrina deformans*	Resistance is moderately heritable and polygenic (Monet 1985, Ritchie and Werner 1981); highly resistant cultivars identified (Ackerman 1953, Simeone 1985)
Powdery mildew *Sphaerotheca pannosa* *Podosphaera clandestina*	Resistance controlled by two loci, with one locus for high resistance (D'Bov 1983); resistance is dominant (Pukanova et al. 1980), few cultivars are highly resistant (Scorza and Okie 1989)
Virus	
Plum pox (PPV)	Little resistance in most cultivars, but sources of resistance exist (Rankovic and Sutic 1980, Surgiannides and Mainou 1985)
Nematode	
Root-knot *Meloidogyne* ssp.	Two dominant resistance genes identified to *M. javanica* (*Mj1* and *Mj2*) (Sharp et al. 1970); a single, dominant resistance gene identified to *M. incognita* (*Mi*) (Weinberger et al. 1943)
Root lesion *Pratylenchus* sp.	Little resistance in most cultivars, but tolerance has been reported (Potter et al. 1984)
Insect	
Green aphid *Myzus persicae*	A single dominant resistance gene identified (*Rm1*) (Monet and Massonie 1994)
Peach tree borer *Synanthedon exitiosa*	Little resistance in most cultivars, but modest resistance has been reported (Chaplin and Schneider 1975, Weaver and Boyce 1965)

Bacterial spot causes severe defoliation and blemishing of fruit, particularly in areas with high rainfall, strong winds, high humidity and sandy soil. There is considerable variation in disease incidence from year to year, and under favorable conditions for infection all cultivars show at least some symptoms, although highly resistant cultivars have been identified (Keil and Fogle 1974, Simeone 1985, Werner et al. 1986). Cultivars in the eastern U.S.A. tend to be more resistant than those in the west; the breeding program in North Carolina has been particularly successful in developing resistant cultivars. Sherman and Lyrene (1981) suggest that resistance is regulated by dominant genes. The PR defense genes, β-1,3-glucanases have been shown to be induced by inoculation with *Xanthomonas campestries* pv. *pruni* (Thimmapuram et al. 2001).

Peach leaf curl is a problem in many peach growing regions. Resistant cultivars have been identified, but immunity has not been reported (Ritchie and Werner 1981, Simeone 1985). Leaf curl resistance in peach is moderately heritable and likely under polygenic control (Monet 1985, Ritchie and Werner 1981). Tolerance to the disease is in a large part dependent upon whether the genotypes begin to leaf-out when conditions are optimal for infection (Ackerman 1953), although there are resistant genotypes that leaf-out under conditions favorable to infection (Ritchie and Werner 1981, Scorza 1992). Eglandular leaf genotypes appear to be more resistant than glandular ones, and nectarines are less susceptible than peaches.

Powdery mildew frequently attacks leaves, young shots and fruits. Mildew resistance appears to be regulated by two loci with one providing strong resistance, and another conditioning intermediate to low resistance (D'Bov 1983, Pukanova et al. 1980). The high resistance found at the first locus is epistatic to moderate and low resistance at the other locus. The allele for moderate resistance is dominant to low resistance. While strong resistance exists in *P. persica*, high levels have only been incorporated into a few cultivars (Scorza and Okie 1990).

Leucostoma or peach canker is a particularly serious disease in northern production areas, where tissue death during the winter serves as an entry point for the pathogen. This canker kills scaffold limbs and ultimately the whole tree. High levels of resistance have not been found among North American cultivars, but resistance does exist in Chinese and Russian germplasm (Gairola and Powell 1970, Hampson and Sinclair 1973, Scorza and Pusey 1984). Resistance to canker appears to be strongly correlated with cold tolerance (Chang et al. 1989) and how well water transport is maintained through the canker zone (Chang et al. 1991).

Fungal gummosis causes severe problems in Australia, China, Japan and the southeastern U.S.A. Most cultivars are highly susceptible, but a few have been identified that are highly resistant (Daniell and Chandler 1982, Okie and Reilly 1983). The genetics of resistance is unknown.

Bacterial canker has been associated with the short life syndrome of peach in the southern U.S.A. (Scorza and Okie 1989). Strong resistance to this disease has not been identified, but moderately resistant cultivars have been found with unspecified genetics (Gardan et al. 1971, Weaver et al. 1979).

Brown rot is a serious disease wherever peaches are grown. Little resistance has been described, although feral peaches in Central Mexico and perhaps the Brazilian cultivar 'Bolinha' have some degree of resistance (Feliciano et al. 1987, Scorza and Okie 1989). 'Bolinha' may not be a useful source, as its resistance is limited to the epidermis and it carries several negative characteristics that are readily transmitted such as a tendency for pre-harvest drop, yellow green epidermis and a susceptibility to bruising (Gradziel 1994, Gradziel and Wang 1993).

A number of serious virus diseases and phytoplasm attack peach including plum pox (PPV), prune dwarf, peach yellows, X-disease, *Prunus* necrotic ringspot, tomato ringspot, peach stunt, willow twig, stubby twig, and peach rosette mosaic. No immunity has been reported to any of these diseases, although large differences in resistance to PPV among genotypes have been found (Rankovic and Sutic 1980, Surgiannides and Mainou 1985).

Peachtree borer is a widespread problem and a tree (particularly young trees) can be girdled and killed in a single season. A few cultivars have been identified that are less susceptible than others to infestation, but no strong resistance has been identified (Chaplin and Schneider 1975, Weaver and Boyce 1965).

Myzus persicae is an aphid species that commonly attacks peach. They damage new growth through their feeding, but more importantly, they are vectors of PPV which causes substantial crop loss. Resistant cultivars and genotypes have been identified (Massonie et al. 1982), and Monet (1985) showed that the resistance is controlled by a single dominant gene. Seedlings carrying this gene are resistant to *Myzus persicae* and *M. varians*, but not *Hyalopterus amygdale* (Massonie et al. 1982). Since PPV is transmitted by aphid probing and not feeding, it is not clear if aphid resistance would affect PPV infection and the spread of the disease.

Several nematodes are commonly associated with peaches across the world and can cause replant problems including *Pratylenchus* ssp. (root lesion nematode), *Xiphinema* spp. (dagger nematode), *Meloidogyne incognita* (root knot nematode) and *Criconemella* spp (ring nematode). Tolerance has been reported to *Pratylenchus*, but not immunity (Potter et al. 1984). Multiple resistance genes to *Meloidogyne incognita* have been identified in peach (Gillen and Bliss 2005). Resistance to *M. javanica* has also been described that may be regulated by duplicate, independent dominant factors (Sharp et al. 1970).

Peach tree short life (PTSL) syndrome is a nematode-related disease syndrome of peach caused by a complex of biotic, abiotic and climatic factors. It affects more than 70% of the peach acreage in the southeastern US. It appears to be due to the extreme physiological stress associated with very high densities of ring nematodes, which results in wilting and a sudden collapse of new growth. Tolerance to this disease was unknown until the recent release of the rootstock 'Guardian' (BY520-9). The genetics of tolerance appears to be complex, as 38 AFLP markers have been associated with the PTSL syndrome, on five peach linkage groups (Blenda et al. 2007).

9.5.2 Morphological and Physiological Traits

Trees that have a thrifty growth habit which can be easily picked and pruned in high density orchards are an important goal of most breeding programs. A number of single, recessive genes have been identified that cause extreme size reduction – dwarf (*dw*, dw_2, *dw3*), semi-dwarf (*n*), compact (*ct*) and bushy (*bu1* and *bu2*) (Table 9.5), but few commercial cultivars have been developed from these to date, due to poor

Table 9.5 Genetics of adaptation, productivity, plant habit and fruit quality in peach

Attribute	Observations and source
Adaptation	
Chilling requirement	Generally quantitatively inherited, although a few major genes may exist (Lesley 1944, Sharp 1961); a single, recessive gene for evergreen has been identified (*evg*) (Rodriguez et al. 1994); chilling requirements of buds and seed germination are correlated (Rodriquez and Sherman 1985)
Cold hardiness	Quantitatively inherited, largely additive (Mowry 1964); tissues vary in their hardiness (Cain and Anderson 1980); extremely cold hardy germplasm has been identified (Layne 1992, Myers and Okie 1986, Young 1987)
Season of flowering	Considerable variability exists among genotypes, but genetics is complex and quite subject to environmental interactions (Scorza and Sherman 1996)
Harvest date	Quantitatively inherited, with many major genes (Bailey and Hough 1959, Hansche et al. 1972, Vileila-Morales et al. 1981); a gene has been identified (*sr*), that greatly slows ripening (Ramming 1991)
Flower traits	
Flowers per bud	Single genes have been identified for single/double (*Sh/sh*) (Lammerts 1945)
Flower buds per node	Germplasm with high flower density has been identified (Okie and Werner 1990, Werner et al. 1988)
Petal color	Single genes have been identified for colored/white (W/w), anthocyanins/anthocyaninless (*AN/an*), dark pink/light pink (P/p) and pink/red (R/r) (Lammerts 1945, Monet 1967)
Petal number	Single genes have been identified for single/double (*Di/di*) and fewer extra petals/more extra petals (*Dm1/dm1* and independent *Dm2/dm2*) (Lammerts 1945, Yamazaki et al. 1987)
Petal size	Single genes have been identified for nonshowy/showy (*Sh/sh*) and large showy flowers/small showy flowers (*Sh/sh*) (Lammerts 1945)
Pollen fertility	Single genes located for pollen fertile/pollen sterile (*Ps/ps* and Ps_2/ps_2) (Scott and Weinberger 1944, Werner and Creller 1997)
Leaf traits	
Color	Single gene identified for red leaf/green leaf (*Gr/gr*) (Blake 1937); dominance is incomplete (Chaparro et al. 1995)
Foliar glands	Single genes identified for glandular foliage/eglandular foliage (E/e) (Conners 1922)
Shape	Single genes identified for smooth leaf margin/wavy leaf margin (*Wa/wa*) and normal/willow leaf (*Wa2/wa2*) (Chaparro et al. 1994, Scott and Cullinan 1942,)

Table 9.5 (continued)

Attribute	Observations and source
Plant habit	
Shape	Several single, recessive genes have been identified that influence plant shape – weeping, *pl* (Monet et al. 1988); compact, *ct* (Mehlenbacher and Scorza 1986); pillar, *br* (Scorza et al. 2002); bushy, *bu1* and *bu2* (Lammerts 1945)
Tree Height	Several single, recessive genes have been identified that influence plant height – dwarf, *dw* (Monet et al. 1988), dw_2 (Hansche 1988), *dw3* (Chaparro et al. 1994); semi-dwarf, *n* (Monet and Salesses 1975)
Fruit quality	
Acidity	Quantitatively inherited (Hansche et al. 1972); a QTL has been found for a single locus (D/d) that regulates low vs. high malic acid (Dirlewanger et al. 2004)
Flesh texture	Three single genes regulate melting flesh/ non-melting flesh (F/f), soft melting flesh/firm melting flesh (M/m) (Bailey and French 1941 and 1949) and melting flesh/ stonyhard flesh (*Hd/hd*) (Yoshida 1970); known dominance relationships are $ST > M > m$, F/f and M/m are on the same linkage group (Dirlewanger et al. 2004); candidate gene (endopolygalacturonase) identified for melting vs. non-melting trait (Peace et al. 2005b)
Pit adherence	Single gene regulating the freestone/clingstone trait (F/f) (Bailey and French 1941 and 1949); QTL identified located on same linkage group as the flesh texture genes *M/m and St/st* (Dirlewanger et al. 2004)
Internal breakdown (IB)	High heritability exists for all the traits associated with IB including mealiness; flesh browning and flesh bleeding; QTL have been found for all of these characteristics (Peace et al. 2005, 2006); the pectic enzyme polygalacturonase (PG) is strongly associated with the melting flesh characteristic and IB (Lester et al. 1996, Peace et al. 2006, Pressey and Avantes 1978)
Pubescence	Single genes regulating pubescent skin/glabrous (G/g) (Blake 1932) and normal pubescence/rough surface (Okie and Prince 1982); level of pubescence is quantitatively inherited (Blake 1940, Weinberger 1944)
Color	A number of single genes regulating color have been identified including *Y* which results in white fruit (Conners 1922), *h* which suppresses red color (Beckman et al. 2005) and *fr* which regulates full red color (Beckman and Sherman 2003); *bf* (blood flesh) is regulated by a single gene (Werner et al. 1998); degree of red skin color is likely regulated quantitatively; red color around the pit is dominant (Blake 1932)
Overall fruit quality	Browning, soluble solids, sweetness and overall flavor are quantitatively inherited (Hansche et al. 1972, Hansche 1986, Hansche and Boynton 1986)
Shape	Mostly quantitatively inherited, but a single, dominant gene has been identified for saucer vs. non-saucer shape (Lesley 1939) that is lethal in the homozygous state (Guo et al. 2002)
Size/weight	Quantitatively inherited with mostly additive genes (Hansche et al. 1972, Weinberger 1955)

fruit quality and issues associated with short internodes and large numbers of spurs (Loreti and Massai 2002). Greater success in developing cultivars for high density plantings has come from the use of genes that modify plant shape. The pillar gene (*br*), which forms a columnar growth habit, has been successfully used in the U.S.A. and Italy to produce a narrower tree that is easier to prune (Fig. 9.1). The weeping gene (*pl*), is also being utilized by the French to develop more efficiently pruned trees, although specific orchard systems will need to be developed to exploit this habit. A potentially useful 'arching' phenotype with a distinctive curvature of the one-year-old shoots has been described in Brbr/plpl genotypes (Werner and Chaparro 2005).

The environmental adaptations that have received the greatest amount of attention from peach breeders are winter cold hardiness, spring frost hardiness and chilling requirement. Cold hardiness is an issue in the cold temperate zones where peaches have been traditionally grown, and reducing the chilling requirement has become very important in expanding the range of peach cultivation into warmer climates. Frost tolerance has been an issue in both warm and cold climates. Winter cold tolerance is influenced by when cold tolerance is initiated, the rate of development of cold tolerance, the maximum cold tolerance that can be achieved, when cold tolerance is lost, the rate of loss of tolerance, and whether cold tolerance can be regained (Stushnoff 1972). The avoidance of spring frost damage can be achieved by developing cultivars with late blooming dates and multiple flowers per node. Later blooming types are less likely to suffer spring frosts and those with higher

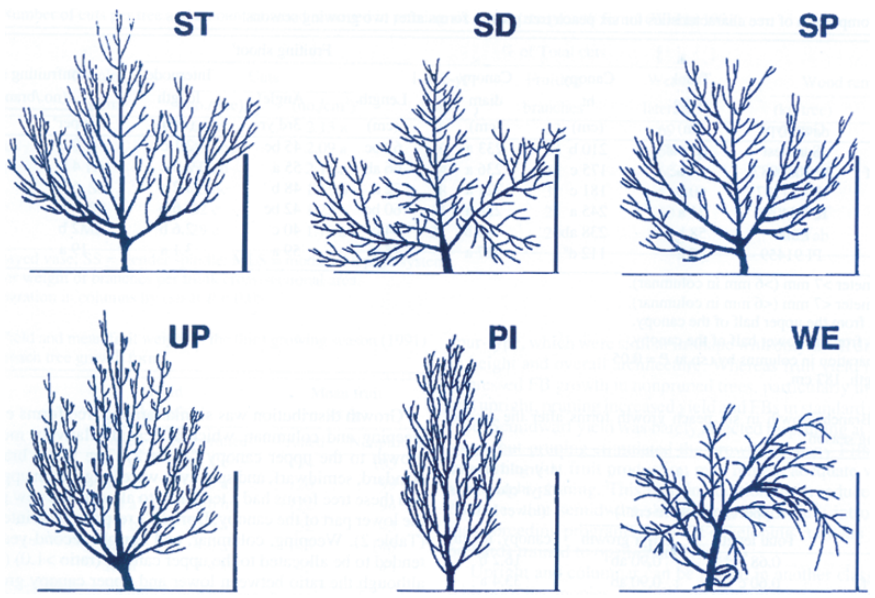

Fig. 9.1 Standard (ST), semidwarf (SD), spur-type (SP), upright (UP), pillar (PI) and weeping (WE) peach tree growth habits from Bassi et al. 1994

flower numbers are more likely to have sufficient numbers of flowers remaining after frosts. Cultivars that receive inadequate chilling commonly display sporadic foliation, irregular flower formation and floral abscission. Most peach cultivars have chilling requirements (hours below 7° C) of 650–1000 hrs, but germplasm has been utilized to produce cultivars with chilling requirements as low as 150 hours.

Most of the information available on cold tolerance has come from natural freezes during test winters, although methods of conducting controlled freezes have been developed (Layne 1989, Quamme 1991, Wisniewski and Arora 1991). Genotypes with high chilling requirements tend to have the least bud death due to winter cold. In general, a range in bud damage is apparent in segregating populations, suggesting quantitative inheritance; however, some segregating populations are skewed and have greater average resistance to cold injury than would be predicted by examining the parents (Mowry 1964). 'Redskin' stood out as a genotype with only modest hardiness that produced many progeny with good bud tolerance to cold. Few studies have sought to isolate the genes associated with cold tolerance in peach, although transcripts of the stress-induced dehydrin gene (*ppdhn1*) have been found to accumulate more in cold-tolerant peach tree cambium than the low cold tolerant 'Evergreen' cultivar (Artlip et al. 1997, Wisniewski et al. 1999).

Many of the genotypes most resistant to mid-winter cold originated from northern China such as 'Chui Lum Tao', 'Hui Han Tao', 'Tzim Pee Tao' and 'Siberian C'. Most of these hardy types have early bloom dates and poor fruit quality which take 3 or 4 generations of backcrossing to breed out, with the subsequent loss of some winter hardiness (Scorza and Sherman 1996). Unusually cold tolerant naturalized North American hybrids with late bloom have also been identified such as 'Reliance' (Cain and Anderson 1980, Layne 1984).

Considerable variability has been observed in numbers of flower buds per node that is stable across years and locations (Okie and Werner 1990) and is highly heritable (Hansche et al. 1972) (Fig. 9.2). Those cultivars developed for the colder climates tend to have higher numbers of buds per node than those developed in warmer climates (Werner et al. 1988). The number of flowers and fruits on 2-year old seedlings has also been shown to be heritable at the $h^2 = 0.16$ and $h^2 = 0.33$ level, respectively (Hansche 1986). While large numbers of flowers are of value in years of frost damage, in the absence of such damage, excessive flowering requires increased thinning and can negatively affect fruit size.

Little work has been conducted to determine the genetics of chilling hour requirements, although segregation patterns suggest that it is a quantitative trait, with a few major genes having important effects (Lammerts 1945, Lesley 1944, Sharp 1961). The inheritance appears to be largely additive, with little dominance effects. The genes regulating a low chilling requirement have come predominately from peaches from south China (Sharp 1974). Lammerts (1945) identified a recessive gene for 'evergreen' that held most of its foliage during mild, frostless winters. More recent work has shown that the wild type gene is incompletely dominant with heterozygotes being intermediate (Rodriquez et al. 1994). This gene now referred to as *Evergrowing* has been mapped (Wang et al. 2002a) and shown to be a result of a deletion in a MADS-box transcription factor sequence(s) (Bielenberg et al. 2004).

Fig. 9.2 High (*top*) and low (*bottom*) flower bud density in peach seedlings

The genetics of bloom date is largely unknown, although Hansche et al. (1972) did show that this trait was moderately heritable at $h^2 = 0.39$. While considerable variability has been described, it has proven difficult to partition the relative effects of chilling requirement, rate of bloom development and environment. There is likely an interaction between cold and heat requirements and the conditioning of other genes appears important. Regardless, cultivars do maintain 'a rather ordered progression of bloom at any given locality' (Scorza and Sherman 1996), making local selection possible.

Much more is known about time of fruit maturity. Considerable variability is found in this trait and it is quantitatively regulated with a very high heritability (Hansche 1986, Hansche et al. 1972). Bailey and Hough (1959) presented a model that involved 9 major or dominant genes and 10 modifying genes. Vileila-Morales et al. (1981) found that early fruiting is regulated by three major genes.

A number of simply inherited foliar and flower traits have been described. Among the foliar traits are red leaf/green leaf (*Gr/gr*), smooth leaf margin/wavy leaf margin (*Wa/wa*), Willow-leaf (*Wa2/wa2*) and glandular foliage/eglandular foliage (*E/e*). *E* has been located on Linkage group 7 (Dirlewanger et al. 2004). Among the

flower traits are pollen fertile/pollen sterile (*Ps/ps* and Ps_2/ps_2), nonshowy/showy (*Sh/sh*), large showy flowers/small showy flowers (L/l), colored/white (W/w), with anthocyanins/anthocyaninless (*AN/an*), dark pink/light pink (p/p), pink/red (R/r), single/double (*Di/di*) and fewer extra petals/more extra petals (*Dm1/dm1*and independent *Dm2/dm2*) (Fig. 9.3). Two pairs of these loci have been shown to segregate independently, E/e – Ps/ps and Sh/sh – An/an (Monet and Bastard 1983, Monet et al. 1985).

9.5.3 Fruit Quality

Numerous traits related to fruit quality are of importance to peach breeders. In the fresh market, consumers desire a large, well shaped fruit that is flavorful with a high sugar content and low to moderate acidity. For the processed market, several characteristics are appreciated including firm flesh, absence of a tip on the pit, no pit cracking, attractive color and non-browning of the flesh.

A number of single genes have been described that regulate important fruit characteristics (Table 9.5). Bailey and French (1941 and 1949) identified genes for freestone/clingstone (F/f), melting flesh/non-melting flesh (M/m) and soft melting flesh/firm melting (*St/st*) which are all found on the same chromosome. The dominance relationships between the genes regulating flesh texture are $ST > M > m$. *F* appears to be epistatic to *mm* allowing for only *St* or *M* expression, although F_mm could be lethal (Scorza and Sherman 1996). Only a single freestone, non-melting individual has been reported and it has been lost (Blake 1937). Yoshida (1970) described genes for melting flesh/'stonyhard' flesh (*Hd/hd*); these plants produce little ethylene and remain firm throughout storage (Goffreda 1992, Haji et al. 2001).

A significant recent effort has been undertaken at the University of California, Davis to describe the genetics of a number of traits associated with internal breakdown (IB) of fruit or chilling injury (Peace et al. 2005, 2006). Using a combination of conventional and QTL mapping approaches, they have found high heritability for all the traits associated with IB including mealiness, flesh browning and flesh bleeding and found major QTL for all of these characteristics. The observed segregation patterns suggested that only a few major genes control each of the IB symptoms. Mealiness and browning were positively correlated, and both were negatively associated with bleeding (red coloration). Mealiness and bleeding were positively correlated with flowering date, while browning was positively associated with harvest date. The flesh color locus *Y* did not have a significant effect on IB.

The expression of a number of genes has been associated with the ripening and softening of peach fruits. Several cell hydrolases that cause cell wall-loosening have been implicated in fruit softening including glucanases, cellulases and pectic enzymes (Bonghi et al. 1998, Callahan et al. 1991, Scorza 2001). Three forms of the pectic enzyme polygalacturonase (PG) have been found in peach fruits, two being

Fig. 9.3 A sample of peach flower types: showy single (*upper left*), non-showy (*upper right*), double showy (*middle right*), double showy extra petals (*middle left*), 'chrysanthemum' petals (*lower left*), variegated petals (*lower right*). Photos by D. Hu and R. Scorza

exo-PG and one being endo-PG. The exo-PG activity is ripening regulated (Downs et al. 1992) and high activity in this enzyme is strongly associated with the melting flesh characteristic (Pressey and Avantes 1978). Lester et al. (1996) found an RFLP for an endo-PG that co-segregated with the melting flesh trait, and they discovered that there was a deletion of endo-PG-related sequences in the nonmelting flesh variety, Fla. 9-26C. Peace et al. (2005) concluded that a single locus with at least one gene for endopolygalacturanase controls the freestone and melting traits with at least three alleles.

When Peace et al. (2006) used a candidate gene approach to identifying specific genes associated with IB, they discovered that a gene encoding endopolygalacturonase co-segregates with the freestone and melting flesh traits and they found a large QTL for mealiness. Endo-β-1,4-glucanases (ppEG1) have been shown to accumulate during fruit abscission and share 76% homology with ripening-related avocado glucanase (Trainotti et al. 1997).

The expression of several genes has been associated with the ethylene climacteric in peach. 1-Aminocyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase activity have been shown to increase during fruit ripening (Callahan et al. 1993a,b). Two ethylene receptor genes, *Pp-ETR1* and *Pp-ERS1*, have been isolated from peach that are homologous to *ETR1* and *ESR1* in *Arabidopisis* (Bonghi et al. 2002). The level of expression of *Pp-ETR1* was unchanged during ripening, while *Pp-ERS1* expression increased in conjunction with the ethylene climacteric. Application of the ethylene inhibitor 1-methyl-cyclopropane reduced expression of both genes, along with ethylene biosynthesis. Ruperti et al. 2001 found two ACC oxidases to be differentially expressed in flowers, fruits and leaves; one of the genes (*PP-ACO2*) was expressed only in fruit and was not affected by propylene, while the other gene (*PP-ACO1*), was highly expressed in senescing leaves, abscising fruit and ripe mesocarp and was positively regulated by propylene. The transcripts from three genes, *PpAz8*, *PpAz44* and *PpAz152* have been isolated from cells of fruit and leaf abscission zones that show homology to PR thaumatin-like proteins and plant and fungal β-D-oxylosidases (Ruperti et al. 2002).

In other genetic work on the biochemical components associated with fruit ripening and taste, Monet (1979) described a gene pair (D/d) that determines low malic acid vs. normal. Initial studies suggested that low fruit acidity was dominant to high acidity, but subsequent work has shown a continuous range of variability. Hansche et al. (1972) found a modest level of heritability for fruit acidity ($h^2 = 0.19$), while heritability for fruit soluble solids was only 0.01. Fruit browning was shown to have a heritability of 0.35 in another study of peach (Hansche and Boynton 1986). Ramming (1991) identified a gene, *sr*, that slows down fruit ripening. Genotypes that are homozygous for this gene ripen very slowly or not at all, have reduced CO_2 and C_2H_4 production and fail to abscise. Hansche (1986) found low to medium heritability for soluble solids, sweetness, firmness and flavor in peach and nectarine populations dwarfed by the *dw* gene. Etienne et al. (2002) cloned six peach genes associated with organic acid metabolism and storage during fruit development (Mitochondrial citrate synthase, cytosolic NAD-dependent malate dehyrogenase, vacuolar proton translocating pumps, vacuolar H+-ATPase, and two vacuolar H+-pyrophophatases).

Several compounds have been found in peach that can cause food allergies, including a family of 9 kDa lipid transfer proteins (LTPs) (Malet et al. 1988, Pastorello et al. 1999). These compounds cause type I allergic reactions in humans by binding to immunoglobin E. Transcripts of two LTP genes, *pp-LTP1* and *pp-LTP2*, are found in peach with *pp-LTP1* being expressed in the skin of ripe fruit, while *pp-LTP2* expresses in the ovary (Botton et al. 2002).

Blake (1932) described a gene pair regulating pubescent skin/glabrous (G/g). Heavy pubescence was initially reported as being dominant to light pubescence (Blake and Connors 1936), although the amount of pubescence appeared to be quantitatively inherited in later studies (Blake 1940, Weinberger 1944). Most recently, Okie and Prince (1988) have reported on a gene regulating normal pubescence vs. a rough surface (*Rs/ss*) that also causes glabrous flower buds. Interestingly, it is not expressed in *gg* genotypes.

Conners (1922) and Blake (1934 and 1940) originally suggested that small fruit size was dominant to large fruit size, but later work has indicated that fruit size is controlled by predominantly additive genes with little dominance involved (Hansche et al. 1972, Weinberger 1955). Scorza and Sherman (1996) suggested that 'unimproved genotypes could express a few genes that have major effects on fruit size'. Hansche (1986) found moderate to high heritability for fruit weight in peach and nectarine populations dwarfed by the *dw* gene.

A single, dominant gene regulating saucer vs. non-saucer shape (S/s) has been identified (Lesley 1939) that is lethal in the homozygous state (Guo et al. 2002), although shape in general appears to be quantitatively regulated (Scorza and Sherman 1996). Oval has been described as dominant to round, but other studies suggested a much more complex inheritance (Blake 1940). The S locus is found on Linkage group 6, along with Dwarf (*Dw*), Redleaf (*Gr*) and male sterility (*ps*) (Fig. 9.2). The D/d locus regulating acid level may also be in this linkage group as Monet et al. (1985) found them to be linked by 30 cM to S/s; however, the D locus was found on Linkage groups 2 and 5 in the composite map (Dirlewanger et al. 2004).

A few single genes have been associated with fruit color. An allele (Y) has been described that produces white fleshed fruit (Connors 1920) and another, highlighter (h), suppresses red color (Beckman et al. 2005). The relationship between these two alleles has not been explored, although highlighter is known to be independent from the petal coloration alleles anthocyaninless (*An*) and white flower (W). The full red color phenotype is regulated by a recessive gene *fr* (Beckman and Sherman 2003), with the degree of red skin color likely regulated by multiple genes with complex environmental interactions. The blood-flesh trait (red-violet mesocarp) is regulated by a single gene, *bf* (Werner et al. 1998). A red surface blush had a heritability of $0.19 + / - 0.04$ in a segregating population of dwarf peaches (Hansche 1986). The degree of red color around the pit varies greatly and is likely polygenic; however, the presence of red color has been reported to be dominant (Blake 1932). Pillar (*Br*), double flowering and the flesh color locus are linked (Rajapakse et al. 1995).

French (1951) studied the segregation of several traits in hybrid peach populations including pubescence, flesh stringiness, coarseness, stone size, juiciness, skin

thickness and toughness. French's populations varied greatly between years making conclusions difficult, but he did suggest that stringiness of the flesh and flesh coarseness were mostly recessive to their counterparts. Expression of the juiciness trait and stone size was very dependent on which parents were crossed; some parents appeared to pass the trait in a dominant fashion, although inheritance generally appeared to be quantitative. The thickness of the skin of progeny populations was dependent on the parents. A statistical analysis that estimates both environmental and genetic components of variability needs to be made to better elucidate the genetics of these traits.

9.6 Crossing and Evaluation Techniques

9.6.1 Pollination and Seedling Culture

Pollen is generally collected from well advanced flowers that are not quite open ('balloon stage'). The flowers are usually collected in paper bags, and the anthers are extracted within a few hours of collection by rubbing them over a wire mesh screen with a 4–6 mm mesh. When the flowers must be stored for longer periods of time, they can be held in the collection bags at 2° C–4° C for a couple of days. The anthers are most often sifted onto absorbent paper for drying and allowed to dehisce for 12–24 hours at ambient room temperature. After drying, the pollen is commonly placed into glass shell vials and can be held at ambient temperature for a season. For longer storage times, the pollen is generally frozen at −18°C (Griggs et al. 1953) or held at 0°C–2°C at 25% relative humidity (King and Hesse 1938). Pollen frozen in liquid nitrogen will retain its viability for many years.

Stamens of peach flowers are attached distally in a ring at the base of the corolla and can be easily removed by pulling the flowers apart using the finger nails. Emasculation is done when the flowers approach anthesis but are not yet open or shedding pollen. Branches are emasculated from the top down, to avoid accidental wind pollination and checked every few days for 7–10 days after pollination to remove any new flowers.

Pollination is accomplished using a camel's hair brush, the rubber tip of a pencil, a finger or a glass rod. A simple touch of the stigmatic surface is all that is necessary. After pollination, 70% alcohol is used to kill any pollen left on the applicator. Pollinators are generally not attracted to petaless flowers, so branches are not generally covered for cultivar development crosses. For genetic crosses, chance pollination is prevented by covering the branches with paper bags or cheese cloth. If wet weather is expected, the paper bags can be protected with polyethylene bags, but they need to be well ventilated by punching holes in them. To protect against frost damage during and after pollination, plastic houses or parachute covers with heat sources have proven effective (Werner and Cain 1985).

Seed are collected from ripe fruit soon after harvest, but before they begin to rot or ferment. Seed are commonly allowed to dry after removal, but the percentage of germination can sometimes be increased by stratifying them before they dry. Stratification is often accomplished by placing a single row of seeds (removed from the endocarp) on the bottom of 250 ml Erlenmeyer flasks and covering them with water containing a fungicide. The next day enough water is removed to uncover the seeds and the flask is stoppered with cotton, film or foil and held at 2° C–4° C (with occasional watering). Seeds are also sometimes stratified in moist perlite in plastic bags with a fungicide. Germination normally begins after 90–120 days, when the rest requirement of the seeds has been met (Hartmann and Kester 1959). Non-germinated seeds can be placed back in cold stratification. When the radicals are 0.5–1 cm long, the seeds are ready for planting. They can be set directly in the field by placing the radical at 5 cm depth, or they can be grown in a greenhouse to get better emergence and early growth. When this is done, the seedlings are generally moved to the field when convenient.

Peach breeders commonly use embryo culture to germinate seed from early-maturing genotypes, particularly in subtropical areas where short development periods are a major goal. Commonly, the flesh of the early ripening types matures before the embryo is fully developed.

Almost all cultivars ripening 70–75 days from full bloom can be successfully cultured, but the culture of younger embryos is dependent on genotype and growth conditions. An index called PF_1 (embryo length/seed length) was proposed by Hesse and Kester (1955) to measure comparative embryo development. In their work, embryos with a PF_1 lower than 70 were difficult to culture, although Ramming (1990) was able to culture embryos at PF_1 as low as 25.

For embryo culture, the fruit are generally surface sterilized with 0.25–1% sodium hypochlorite and the seed is removed from the endocarp. The embryo is then excised from the seed and cultured on 0.6–0.7% agar containing 2–4% sucrose and nutrients (Ramming 1985, Tukey 1934).

9.6.2 Evaluation Techniques

Most commonly, seedlings are planted at 1–2 m within rows and 3.0–4.5 m between rows in the spring following hybridization. Seedlings begin to fruit 1–2 years after planting. High density plantings have also been developed in Florida where seedlings are set at 13 cm apart in rows 1 m apart in August or September in the same year as hybridization (Sherman et al. 1973). This system allows for many more seedlings to be evaluated in small areas of field space, but only the most easily scored traits such as chilling requirement, fruit development period and fruit quality can be successfully evaluated (Rodriquez et al. 1986). The less dense plantings are typically evaluated for four or five years with little yearly rouging of undesirable genotypes, while the high density plantings are evaluated for three years with thinning in the second year.

Selections that appear to have potential are then second tested under commercial field conditions against standard cultivars. The most promising ones are distributed after 2–4 crops to a number of test locations within the expected adaptation zone, including grower cooperators and Agriculture Experiment Stations. When a selection survives these tests by showing high commercial potential, it is released. A minimum of 10 years, and often many more, are required between the initial cross and a genotypes release to the industry.

9.7 Biotechnological Approaches to Genetic Improvement

9.7.1 Regeneration and Transformation

Peaches have been regenerated utilizing several systems including in vitro leaves (Gentile et al. 2002), mature cotyledons (Pooler and Scorza 1995), embryo-derived callus (Scorza et al. 1990) and immature zygotic embryos (Hammerschlag et al. 1985). However, there are only two reports of stable peach plant transformation. Smigocki and Hammerschlag (1991) generated transgenic peach plants from embryogenic cultures of 'Redhaven' using the sooty mutant strain of *A. tumefaciens, tms*:328::Tn5. This strain carries an octopine type Ti plasmid with a functional cytokinin gene and a mutated auxin gene. The transgenic plants with the cytokinin gene were dwarf, produced unusually high numbers of branches and had delayed leaf senescence (Hammerschlag et al. 1997, Hammerschlag and Smigocki 1998). Perez-Clemente et al. (2004) produced transformants using embryo explants from stored seeds, utilizing two strains of *A. tumefaciens* containing the binary plasmid pBIN19 with the CaMV35spor-sGFP-CaMV35ster cassette as a reporter gene. Their highest efficiency rate of transgenic plant production was 3.6%, utilizing *A. tumefaciens* strain C58 and embryo sections. Between these two reports of preach transformation it appears that a total of four transgenic peach plants have been produced. To date there have been no reports replicating these results. An efficient, repeatable peach transformation methodology awaits development.

Efforts are underway to improve peach transformation protocols. For example, Padilla et al. (2006) conducted a large multivariate experiment to determine the optimal conditions for *Agrobacterium*-mediated transformation of peach explants. The GUS (*uidA*) marker gene was tested using two *A. tumifaciens* strains, three plasmids and four promoters, while GFP was evaluated in six *A. tumefaciens* strains, one plasmid and the doubleCaMV35s (dCAMV35s) promoter. The highest rates of transformation were produced with the combination of *A. tumifaciens* EHA105, plasmid pBIN19 and the CaMV35s promoter utilizing peach epicotyl internodes (56.8%), cotyledons (52.7%) and embryotic axes (46.7%). While these studies have enhanced transformation protocols in peach, transformation rates remain rather low and when combined with low regeneration rates the development of transgenic peaches remains problematic.

9.7.2 Genetic Mapping and QTL Analysis

A growing number of molecular linkage maps have emerged of peach and its relatives (Table 9.6); five maps are available of pure *Prunus persica*, two of almond × *P. persica*, two of *P. persica* × *P. davidiana*, and one each of *P. persica* × nectarine, *P. persica* × *P. ferganensis* and myrobalan plum × an almond – *P. persica* hybrid. Map coverage ranges from 396–1300 cM, with 8–23 linkage groups being identified. Molecular markers have also been used to distinguish between peach

Table 9.6 Published genetic linkage maps of peach

Parents	No. Loci	Linkage groups	Size (cM)	Reference
Peaches 'NC174RL' × 'Pillar'	83	15	396	Chaparro et al. 1994
Peaches 'New Jersey Pillar' × 'KV77119'	79	13	540	Abbott et al. 1998, Rajapakse et al. 1995, Sosinski et al. 2000
Peaches 'Suncrest' × 'Bailey'	145	23	926	Abbott et al. 1998, Sosinski et al. 2000
Peaches 'Lovell' × 'Nemared'	153	15	1300	Abbott et al. 1998, Lu et al. 1998, Sosinski et al. 2000
Peaches 'Harrow Blood' × 'Okinawa'	76	10		Gillen and Bliss 2005
Peaches 'Akame' × 'Jueitou'	178	8	571	Shimada et al. 2000 Yamamoto et al. 2002
Peach 'Ferjalou Jalousia' × Nectarine 'Fantasia'	249	11	712	Dirlewanger et al. 2004, 2006
Peach 'Guardian' × 'Nemaguard' (*P. persica* × *P. davidiana*) F_2	171	8	737	Blenda et al. 2007
Almond 'Texas' × peach 'Earlygold' F_2	562	8	519	Aranzana et al. 2002, Dirlewanger et al. 2004, Joobeur et al. 1998
Almond 'Padre' × peach 54P455 F_2	161	8	1144	Bliss et al. 2002, Foolad et al. 1995
Peach 'Summergrand' × *P. davidiana* clone 1908	23, 97[1]	3, 9	159 471	Dirlewanger et al. 1996, Viruel et al. 1998
Peach IF7310828 ('J.H. Hale' × 'Bonanza') × selection of *P. ferganensis* BC_1	216	8	665	Dettori et al. 2001, Quarta et al. 2000, Verde et al. 2005
Myrobalan plum P.2175 × almond – peach hybrid GN22	93, 166[1]	8, 7	525, 716	Dirlewanger et al. 2004

[1] Separate maps were generated for each of the parents

cultivars, measure their relatedness and determine their origins (Aranzana et al. 2004, Dirlewanger et al. 2002, Testolin et al. 2000, Xu et al. 2006).

Linkage relationships with molecular markers have been described for 23 monogenic morphological traits associated with adaptation, flower color, fertility, leaf shape and color, plant habit, fruit quality and pest resistance (Table 9.7). QTL have also been identified for 23 horticulturally important traits including bloom and

Table 9.7 Monogenic traits associated with molecular markers in peach

Trait	Linkage group	References
Adaptation		
Evergrowing (*evg*)	1	Dirlewanger et al. 2004, Wang et al. 2002
Flower traits		
Double flower (*Dl*)	2	Dirlewanger et al. 2004, Sosinski et al. 2000
Flower color (*Fc*)	3	Dirlewanger et al. 2004, Yamamoto et al. 2001
Male sterility (*Ps*)	6	Dirlewanger et al. 1999, 2004, 2006
Leaf traits		
Leaf color (*Gr*)	5	Chaparro et al. 1994, Dirlewanger et al. 2004, Yamamoto et al. 2001
Leaf glands (*E*)	7	Dettori et al. 2001, Quarta et al. 2000
Leaf shape (*Nl*)	6	Dirlewanger et al. 2004
Plant habit		
Dwarf plant (*Dw*)	6	Dirlewanger et al. 2004
Pillar growth habit (*Br*)	2	Dirlewanger et al. 2004
Fruit quality		
Blood flesh (*bf*)	4	Gillen and Bliss 2005
Flat fruit (*S*)	6	Dirlewanger et al. 1999, 2004, 2006
Flesh adhesion (*F*)	4	Abbott et al. 1998, Dettori et al. 2001, Dirlewanger et al. 2004, Quarta et al. 2000, Yamamoto et al. 2001
Flesh color (*Y*)	1	Abbott et al. 1998, Bliss et al. 2002, Dirlewanger et al. 2004, Warburton et al. 1996
Flesh color around stone (*Cs*)	3	Dirlewanger et al. 2004, Yamamoto et al. 2005
Non acid fruit (*D*)	2,5	Bliss et al. 2002, Dirlewanger et al. 1999, Dirlewanger et al. 2004
Polycarpel (*Pcp*)	3	Bliss et al. 2002, 2004, 2006
Skin color (*Sc*)	6	Dirlewanger et al. 2004, Yamamoto et al. 2001
Skin hairiness (*G*)	5	Bliss et al. 2002, Dirlewanger et al. 1999, 2004, 2006
Pest resistance		
Leaf curl resistance	3,6	Viruel et al. 1998
Nematode resistance (*Mij*)	2	Abbott et al. 1998, Dirlewanger et al. 2004, Gillen and Bliss 2005, Lu et al. 1998, Lu et al. 1999, Lu et al. 2004, Wang et al. 2002, Yamamoto et al. 2001
Nematode resistance (*Mja*)	7	Blenda et al. 2002, Dirlewanger et al. 2004, Yamamoto et al. 2001
Powdery mildew resistance	7,8	Quarta et al. 2000, Verde et al. 2002
Resistance gene analogs	Many	Gillen and Bliss 2005, Lalli et al. 2005

Table 9.8 QTL[1] associated with major traits of peach

Trait	Linkage group	References
Adaptation		
Flowering time	4	Dirlewanger et al. 1999, Quarta et al. 2000, Verde et al. 2002
Fruit development period	4	Abbott et al. 1998, Etienne et al. 2002, Verde et al. 2002
Internode length	1	Verde et al. 2002
Maturity date	3, 4	Dirlewanger et al. 1999, Etienne et al. 2002
Productivity	6,9	Dirlewanger et al. 1999
Ripening time	2, 6	Dirlewanger et al. 1999, Quarta et al. 2000, Verde et al. 2002
Short life syndrome	1, 2, 4, 5, 6	Blenda et al. 2007
Fruit quality		
Bleeding	1,4	Peace et al. 2006
Browning	5	Peace et al. 2006
Fruit diameter	2	Abbott et al. 1998
Fruit skin color	2,6	Quarta et al. 2000, Verde et al. 2002
Fruit weight	5, 6	Abbott et al. 1998, Dirlewanger et al. 1999, Etienne et al. 2002
Mealiness	4	Peace et al. 2006
pH	5	Abbott et al. 1998, Etienne et al. 2002
Titratable acidity	5, 6	Bliss et al. 2002, Dirlewanger et al. 1999, Etienne et al. 2002
Malic acid content	5, 6	Dirlewanger et al. 1999, Etienne et al. 2002
Citric acid content	5, 6	Dirlewanger et al. 1999, Etienne et al. 2002
Quinic acid	8	Etienne et al. 2002
Soluble solids	2, 4,6	Abbott et al. 1998, Dirlewanger et al. 1999, Etienne et al. 2002, Quarta et al. 2000, Verde et al. 2002
Fructose content	4	Abbott et al. 1998, Etienne et al. 2002
Glucose content	4	Abbott et al. 1998, Dirlewanger et al. 1999, Etienne et al. 2002
Sorbitol	6	Dirlewanger et al. 1999
Sucrose content	5	Dirlewanger et al. 1999, Etienne et al. 2002

[1]QTL that were identified in more than one year

ripening time, fruit quality, storage life, freestone trait, internode length and pest resistance (Table 9.8).

Considerable synteny has been observed among the maps of the various *Prunus* species, allowing for the development of a *Prunus* consensus map [Cmap in the Genome Database for Rosaceae (GDR) at http://www.rosaceae.org]. When the positions of RFLP, SSR and isozyme anchor markers are compared among the individual genetic maps, the genomes of the diploid species of almond, apricot, cherry, *P. davidiana*, *P. cerasifera* and *P. ferganensis* are mostly collinear (Dirlewanger et al. 2004). Only one large chromosomal rearrangement has been found, a reciprocal translocation in the almond ('Garfi') × peach ('Nemared') cross (Jauregui et al. 2001) and the peach F_2 'Akame' × 'Juseitou' (Yamamoto et al. 2001). A high level of synteny also appears to exist between *Prunus* and *Malus*,

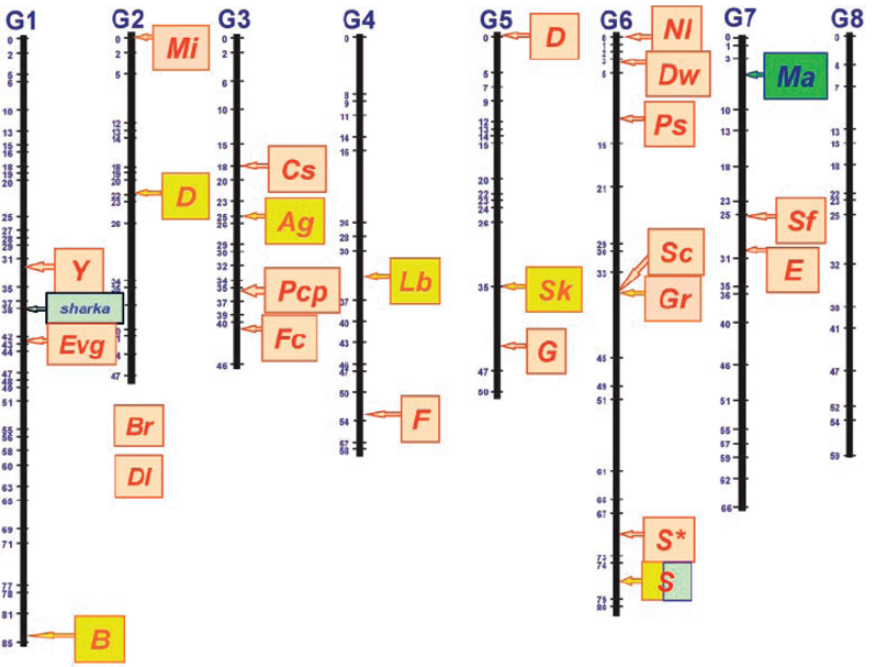

Fig. 9.4 Approximate position of 28 major *Prunus* genes mapped in populations of apricot (blue background), peach (orange background), almond or almond × peach (yellow background), and Myrobalan plum (green background) (Dirlewanger et al. 2004). The gene abbreviations are: *Y*, peach flesh color; *B*, almond/peach petal color; *sharka*, plum pox virus resistance; *B*, flower color in almond × peach; *Mi*, nematode resistance from peach; *D*, almond shell hardness; *Br*, broomy plant habit; *Dl*, double flower; *Cs*, flesh color around the stone; *Ag*, anther color; *Pcp*, polycarpel; *Fc*, flower color; *Lb*, blooming date; *F*, flesh adherence to stone; *D*, non-acid fruit in peach, *Sk*, bitter kernel; *G*, fruit skin pubescence; *Nl*, leaf shape; *Dw*, dwarf plant; *Ps*, male sterility; *Sc*, fruit skin color; *Gr*, leaf color; *S**, fruit shape; *S*, self-incompatibility (almond and apricot); *Ma*, nematode resistance from Myrobalan plum; *E*, leaf gland shape; *Sf*, resistance to powdery mildew. Genes *Dl* and *Br* are located on an unknown position of G2

although only limited numbers of loci have been compared. Dirlewanger et al. 2004 was able to generate a map for all of *Prunus* on which 28 major genes were mapped in populations of apricot, peach, almond and Myrobalan plum (Fig. 9.4).

9.7.3 Genomic Resources

Several bacterial artificial chromosome (BAC) libraries have been developed for peach (Genome Database for Rosaceae (GDR) at http://www.rosaceae.org). Two of the largest are those of Georgi et al. (2002) which was generated from fruit mesocarp of the peach rootstock 'Nemared' and Wang et al. (2001) which was produced from

leaves of the traditional cultivar Jingyu. The libraries of Georgi et al. (2002) and Wang et al. (2001) contain 44,160 and 20,736 clones, respectively.

Over 85,000 *Prunus* ESTs have been sequenced and deposited in the NCBI dbEST database (http://www.genome.clemson.edu/gdr/). A high proportion of the ESTs have been found to contain SSRs in transcribed regions, allowing for the placement of known genes on linkage maps (Georgi et al. 2002, Jung et al. 2005, Wang et al. 2002). The EST-derived SSRs are less polymorphic than those from intergenic regions, but are more easily transferred among species, as the transcribed sequences are often more highly conserved. Most recently,18 EST-SSR markers have been developed from a mesocarp cDNA library of the peach cultivar 'Yumyeong', whose primers gave successful amplification in six other *Prunus* species (almond, apricot, sweet cherry, Japanese plum, European plum and *Prunus ferganensis*) (Vendramin et al. 2007).

Horn et al. 2005 used probes of core markers (141) from the 'Texas' × 'Earlygold' peach map to screen the BAC library to provide the framework for a physical and transcript map. When they hybridized 1,236 ESTs from the unigene set and an additional 68 peach cDNA colonies to genetically anchored BACs, they were able to place 11.2% of the ESTs and cDNAs on the peach genetic map. One cluster of 32 ESTs were of special note as most of them were not homologous to sequences in the NCBI data base. It was suggested by Horn et al. (2005) that these 'ESTs might be unique to fruit trees or rapidly evolved from a common ancestor to fulfill new functions in fruit trees'.

Resistance gene analogs (RGAs) representing NBS-LRR, kinase, transmembrane domain classes, pathogen response (PR) proteins and resistance-associated transcription factors have also been hybridized to the peach BAC library to develop a resistance map for *Prunus* (Lalli et al. 2005). Using the peach physical map data base of the Genome Database for Rosaceae (GDR), 42 map locations were identified with possible resistance regions across 7 of the 8 linkage groups of peach.

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