5 Peach

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5.1 Introduction

5.1.1 Peach [*Prunus persica* (L.) Batsch]

In temperate regions, the family Rosaceae ranks third in economic importance. Its commercially valuable members include fruit producing (e.g., stone fruits, apples, brambles, and strawberries), nut-producing (almond), lumber producing (e.g., black cherry) and ornamental (e.g., roses, flowering cherry, quince, and pear) species. Rosaceae is the type family for the Rosales, the largest order in the Rosidae (Heywood 1978) or Calyciflorae (Benson 1979). It is traditionally divided into four well-defined subfamilies. The genus *Prunus*, within the subfamily Prunoideae, is characterized by species that produce drupes known as "stone fruits" where the seed is encased in a hard, lignified endocarp referred to as the "stone", and the edible portion is a juicy mesocarp. The agriculturally most important stone fruit species are *P. persica* (L.) Batsch (peach, nectarine), *P. domestica* L. (European or prune plum), *P. salicina* Lindl. (Japanese plum), *P. cerasus* L. (sour cherry), *P. avium* L. (sweet cherry), *P. armeniaca* L. (apricot) and almond (*P. amygdalus* Batsch) which is cultivated for its edible seed.

All commercial varieties of peach are *P. persica*, including nectarines that differ from peach in the absence of pubescence on the fruit surface. This character segregates as a simple trait presumably controlled by a single gene or a few closely linked genes.

5.1.2 Center of Origin and History of Dispersal

Peaches originated in China, with a cultivation history of over 4,000 years (Hesse 1975). Peach dispersal followed westward with human migration through trade routes and in the wake of conquering armies found it way to Greece. According to Pliny, peach was cultivated in Greece by 332 BC (Hedrick 1917). From Greece, peaches were further dispersed with expansion of the Roman Empire. The early writings of Pliny, Dioscorides, and Virgil exhibit references to peach and apricot (Hedrick 1917; Cullinan 1937). Peaches were brought to North and South America on the ships of the European explorers and settlers. Due to the fact that stone fruits have the seed encased in a hard, lignified structure (stone) obviates special storage conditions thus facilitating their dispersion over long distances. Peach seeds are viable for a year at room temperature and for several years if refrigerated (Scorza and Sherman 1996).

5.1.3 Peach production

Peach is a temperate fruit crop and is grown on all continents except Antarctica. Generally, commercial production lies between latitudes 30° and 45°. The major limiting factors for expansion of commercial production areas are extreme cold temperatures below −35 °C to −40 °C or insufficient length of cold temperature to satisfy dormancy. Table 1 lists the worldwide production, yield and harvest area for peaches and nectarines.

5.1.4 Breeding

Most major peach producing countries have active breeding programs. To develop a new peach cultivar usually takes 15–20 years and requires: 1) pollen collection from male parents; 2) individual hand emas-

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Table 1. Peach world cultivation statistics (FAOSTAT, http//faostat.fao.org)

Year	2000	2001	2002	2003	2004
Production (Mt)	13,317,455	14,005,372	14,712,287	15,355,170	15,561,206
Yield (Hg/Ha)	104,425	112,320	109,781	109,506	109,409
Area Harv. (Ha)	1,275,308	1,246,920	1,340,153	1,402,221	1,422,293

culation of flowers of female parents; 3) hand pollination; 4) collection of seed from fruit that developed from hybridization; 5) seed stratification and germination; 6) greenhouse or nursery culture of seedlings; 7) field planting of the seedlings; and 8) selection and testing of superior phenotypes. The juvenility period in peach is from 2 to 5 years (Sherman and Lyrene 1983). Maintenance, propagation, and selection of seedlings require a large investment of labor, equipment, materials and space, thus various time and space saving methods required for seedling evaluation include the use of high density fruiting nurseries, cultural manipulation, i.e., grafting seedlings onto mature rootstocks, girdling, growth regulator treatments, breeding with dwarf germplasm, and marker-assisted selection (Hansche and Beres 1980; Sherman and Lyrene 1983; Hansche 1990; Scorza 2003). The evaluation of superior seedling selections is a critical stage prior to cultivar release and requires the multiplication of elites on rootstock and evaluation of yield and horticultural characteristics including fruit quality under conditions simulating commercial production. This process generally requires replication in locations and/or years.

Although many commercial peach cultivars were developed from a restricted germplasm base and peach is predominantly self-fertilizing, they remain fairly heterozygous for many characters as evidenced from character segregation in progeny from self or out crosses with wild germplasm. In most cases the characteristics that are desirable for commercial cultivars, including large fruit size, high coloration of the fruit epidermis, and firmness of the flesh, are recessive (Bailey and French 1949). Therefore, integration of adaptive traits from germplasm requires several rounds of introgressive backcrossing to fix the new trait and regenerate the high quality value traits in the original cultivated parent.

Commercially grown peach cultivars represent only a small fraction of the genetic diversity of this species (Scorza et al. 1985; Mehlenbacher et al. 1990; Scorza and Okie 1990; Scorza and Sherman 1996). One of the major problems confronting the fruit breeding community is the loss of native germplasm through deforestation, urbanization, and lack of funds to support germplasm collection and maintenance in the centers of origin. Additionally, cultivation of high quality stone fruit cultivars displaces the lower quality native landraces that carry many of the locally important adaptive traits further accelerating the loss of genetic variability.

5.1.5 Breeding Goals

5.1.5.1 Disease and Pest Resistance

Peaches are susceptible to numerous pathogens and pests (Bailey and Hough 1975; Hesse 1975; USDA 1976; Mehlenbacher et al. 1990; Scorza and Okie 1990). Several book chapters and review articles have summarized the most important disease problems and have discussed breeding strategies and/or programs aimed at obtaining disease resistance (Bailey and Hough 1975; Hesse 1975; Okie et al. 1985; Layne and Sherman, 1986; Childers and Sherman 1988; Scorza 1991; Scorza and Sherman 1996). With the currently environmentally conscious public, chemical control of pests is coming under close scrutiny. As a result, many pesticides are no longer available to the grower, thus interest in natural resistance or engineered resistance has moved the forefront in breeding programs. This fact further underscores the importance of maintenance and study of natural germplasm resources since many native species carry resistance genes that could be introgressed into cultivated varieties.

Peach genotypes have been screened for resistance or tolerance to ring nematode (*Criconemella xenoplax*) (Okie et al. 1987), a primary factor in Peach Tree Short Life syndrome (PTSL), Cytospora canker caused by *Leucostoma* spp. (Scorza and Pusey 1984; Chang et al. 1989), and brown rot (*Monilinia fructicola*) (Gradziel and Wang 1993). These studies have revealed somewhat low but potentially useful levels

of disease resistance and in the case of tolerance to the ring nematode, rootstocks have been developed from initial isolates of tolerant material that ameliorate the effects of peach tree short life in the southeastern United States. Other studies examining the response of numerous peach and nectarine cultivars to *Stigmina carpophila, Monilinia laxa, Sphaerotheca pannosa, Tranzschelia pruni-spinosae, Taphrina deformans* and *Xanthomonas campestris* pv. *pruni* (Simeone 1985; Werner et al. 1986; Simeone and Corazza 1987; Scorza 1992), found most cultivars susceptible to these pathogens.

Other major pests of peach include fruit feeding insects which reduce fruit quality and marketability and insects which feed on vegetative parts of the tree causing reduced viability, performance and increased risk of fungal, bacterial and viral disease. Only a few cases of insect resistance in cultivated genotypes have been reported (Mehlenbacher et al. 1990; Scorza and Okie 1990).

Soil born pathogens also represent a major problem for peach tree cultivation. Nematodes of several different genera are major pathogens of peaches, these include: the dagger nematode (*Xiphenema* spp.) which is responsible for the spread of tomato ring spot virus, a serious pathogen in peach particularly in the US Mid-Atlantic States; root-knot nematodes (*Meloidogyne* spp.) which severely decrease the performance of the trees; the root lesion nematode (*Pratylenchus* spp.) which is associated with replant problems (Scorza and Okie 1990); and the ring nematode (*Criconemella xenoplax*) a primary factor in Peach Tree Short Life syndrome (Okie et al. 1987).

Plum Pox Virus Plum Pox Virus (PPV), also referred to as "Sharka" disease, is one of the most serious diseases of peach and other *Prunus* trees worldwide.

The "Sharka" disease of fruiting trees is caused by a potyvirus *Plum pox virus*. Like other potyviruses, its genome consists of a single RNA molecule/strain (680 to 900 nm length and 15 nm width) 9,800 nucleotides in length with a MW of 3.5×10^6 daltons. It encodes a VPg protein at the 5′ end and is poly adenylated at the 3′ end. According to the sequence the types of isolates can be divided into D, Dideron and M or Marcus serotypes (Laín et al. 1989; Maiss et al. 1989; Teycheney et al. 1989; Riechman et al. 1992; García et al. 1994; Candresse et al. 1998; Rosales et al. 1998).

The woody hosts for PPV are the *Prunus* species including; plums (*P. domestica*) and Japanese plum (*P. salicina*), the apricot (*P. armeniaca*) and peach (*P. persica*). Almonds (*P. dulcis*) can be infected by PPV but are asymptomatic. New PPV isolates that infect cherries (*P. avium* and *P. cerasus*) have also been described. Kalashyan et al. (1994) described a PPV-C in *P. cerasus* and Crescenzi et al. (1997) a PPV-C strain that infects most of the ornamental and wild *Prunus* species, some that are used as rootstocks for grafting trees such us *P. cerasifera, P. insititia, P. besseyi, P. tomentosa, P. spinosa*.

PPV produces symptoms on leaves and fruits. Symptoms vary according to the species, the isolate and the environmental conditions**.** The symptoms on leaves are chlorotic ring spots with necrosis. Symptoms on fruits appear before ripening, and appear as ring spots and deformations. The flesh appears brown and the pits show yellow ring spots. On plum species the affected fruits sometimes drop before reaching maturity.

As is typical with diseases caused by virusus, adequate procedures are presently not available to control the spreading of the virus on infected trees (Llácer and Cambra1998). Cross protection does not work for PPV strains. The spreading of the virus by aphids in a non-persistent manner makes the chemical control of aphids by spraying ineffective. In short term the control of the diseases relays on removing infected trees and planting virus free trees. In a long term the control will be the replacement of the susceptible varieties by resistant cultivars (Dosba et al. 1991).

Natural Resistance to Plum Pox Virus in *Prunus* Germplasm Resistance to pests and pathogens assumes particular importance when fruit quality is affected. Among virus diseases, Sharka disease is of particular concern as it is completely devastating to productivity and to fruit quality. Several laboratories in Europe examined *Prunus* germplasm for resistance to the virus. From this work, it was reported that a limited number of apricot varieties appear to have natural resistance to this disease including 'Goldrich', 'Stark Early Orange', 'Harlayne' 'Harcot' 'Stella' and 'Henderson' (Dosba et al. 1992; Karayiannis and Maniou 1994; Polak and Kominek 1995).

Evaluation of the susceptibility of plum and peach cultivars to Sharka disease has not resulted in the discovery of resistant cultivars like those in apricot. Introgression in a peach genetic background of the resistance available in a related wild species, *Prunus davidiana* and in some almond cultivars, is in progress through back cross progenies (Kervella et al. 1998; Foulongne et al. 2003; Martinez-Gomez et al., 2004).

Due to variable penetrance of the resistance character, to test a putatively resistant cultivar, one needs four years of monitoring after infection to assess the level of resistance or susceptibility. This slows the breeding process and makes finding new sources of resistance difficult. Therefore, it would be of major importance to develop efficient tools to screen for Sharka resistance, particularly where the resistance is recessive or only partial. These genes could then be pyramided to enhance or complement already existing resistant cultivars produced through conventional breeding or via transgenic approaches (see below). In woody plants, molecular tools can provide early information on the genetics of *Prunus* progenies and enable the use of marker-assisted selection (MAS) methods for more efficiently breeding resistant materials.

5.1.5.2
Environmental Stress Tolerance

Peaches are widely adapted throughout their range, and cultivars developed in one growing area are often utilized in many production regions. One of the most important breeding objectives is the development of varieties that perform well in the extremes of a species cultivation range. Thus, for example, in northern regions greater winter hardiness of both flower buds and whole trees is a major breeding consideration as it is the most important factor limiting production in mid-continent and northern climates (Bailey and Hough 1975; Hesse 1975; Mehlenbacher et al. 1990; Scorza and Okie 1990). Flower bud hardiness in peach has been shown to be a complex quantitative trait (Mowry 1964). Peach avoids low temperature injury through deep supercooling, a physical state that depresses the freezing point of cells. In *Prunus*, the degree of deep supercooling is related to cold hardiness of the xylem and flower buds. Cultivated species generally supercool to a lesser degree than hardy wild species (Quamme et al. 1982).

5.1.5.3
Growth Control

Control of tree architecture is of major concern in many fruit tree breeding programs. Genetic control of tree growth habit reduces the need for pruning and facilitates development of more productive, easily managed high-density production systems (Scorza 1984). In peach, several loci control tree size and canopy architecture producing compact (Mehlenbacher and Scorza 1986), spur-type (Scorza 1987), semidwarf (Fideghelli et al. 1979; Scorza 1984), columnar (Scorza et al. 1989, 2002), dwarf (Lammerts 1945; Monet and Salesses 1975; Hansche 1988;) and weeping (Monet et al. 1988) trees. Currently, identification and manipulation of genes controlling the columnar growth habit is underway through application of peach genomic resources and molecular marker mapping (Rajapakse et al. 1995; Scorza et al. 2002, Dr. Renate Horn, personal communication)

5.1.5.4
Fruit Characteristics

Ultimately, fruit quality drives the market for stone fruits. Breeding programs have produced very high quality fruits at maturity, however for storage and shipping of fruit to non-local markets, these varieties must be picked earlier than full maturity resulting in fruits of lesser flavor and aroma in the market place. This has led to a marked decrease consumption of peaches. In the 1960s the US average per capita consumption of peaches was 4.4 kg (Frecon 1988). In the past 20 years the consumption level has remained at 2.0 kg (Cristoso 2002). In comparison to other fruiting species in Rosaceae, (apples 16 kg/yr/capita) the reduced consumption of peaches is partly due to the marketing of immature fruit (Frecon 1988).

Increased firmness of ripe fruit is one of the major breeding targets in peach. Fruit firmness exhibits quantitative genetic control, however, major genes dramatically affecting fruit firmness were previously described including the stony-hard gene (Yoshida 1976), the slow-ripening genes (Ramming 1991). Several other peach fruit traits such as flesh color, melting flesh, soft melting flesh, freestone, low malic acid, and saucer shape are simply inherited. A more complete discussion of the inheritance of peach fruit quality traits can be found in Hesse (1975) and Scorza and Sherman (1996).

5.2 Construction of Genetic Maps

Although *Prunus* is an economically and biologically important genus, little was known about the genome structure and organization of its members up until the advent of DNA marker technologies. However, peach is considered the best genetically characterized species in the genus, and one of the best genetically characterized fruit trees (Mowrey et al. 1990). With the application of DNA marker technologies to the problem of developing genetic resources in trees,

peach has distinct advantages that make it suitable as a model species for structural, comparative and functional genomics. Peach has a relatively short juvenility period, 2–3 years compared to most other fruit tree species, such as, apple, pear, and citrus that have a juvenile phase ranging from 6–10 years (Sherman and Lyrene 1983). While some *Prunus* species such as cultivated plums and sour cherries are polyploid (Moore and Janick 1975), peach is a diploid with $n = 8$ (Jelenkovic and Harrington 1972) and has a comparatively small genome: 5.9×10^8 bp or 0.61 pg/diploid nucleus (Baird et al. 1994). This is equates to about 290 Mbp, about twice the value for *Arabidopsis thaliana* (Arumuganathan and Earle 1991). Finally, a peach transformation system has recently been reported (Perez-Clemente et al. 2005) indicating that peach transformation technologies are developing and these will be useful for facilitating functional genomic studies.

In addition to the importance of peach as a reference for Rosaceae genomics, the genetics of a large number of genes controlling fundamentally important traits has been described in peach. These include genes controlling flower development, fruit development, tree growth habit, dormancy, cold hardiness, disease and pest resistance. Extensive and detailed molecular genetic mapping efforts are being carried out worldwide, and many of these traits (both single gene and QTL) have been mapped. Thus, through the integrated study of genomics and genetics, peach promises to provide biological insight into many important pathways and genes associated with the growth and sustainability of fruiting trees.

5.2.1 Peach Genetics, a Brief History

The cultivated peach belongs to the Rosaceae family, subfamily Prunoideae, genus *Prunus* and subgenus *Amygdalus*. The peach karyotype consists of a clearly identifiable large submetacentric chromosome, and seven more chromosomes of smaller size, two of them acrocentric (Jelenkovic and Harrington 1972; Salesses and Mouras 1977). Although little is known about the chromosomal level location and organization of gene sequences in peach, recent results with fluorescence in situ hybridization (FISH) in the closely related almond (*P. dulcis*) have enabled detection of each chromosome individually based on chromosome length and the positions of the ribosomal DNA (rDNA) genes (Corredor et al. 2004). It is likely that peach chromosomal organization does not differ significantly from that of the other species of *Amygdalus* since crosses between peach and these closely related species are possible and produce fertile hybrids; including the species *P. ferganensis*, *P. mira*, *P. davidiana*, and *P. kansuensis*, and the cultivated almond. Crosses with species of other subgenera (*Prunophora* and *Cerasus*) such as apricot (*P. armeniaca*), Myrobalan plum (*P. cerasifera*), European plum (*P. domestica*), Japanese plum (*P. salicina*) or sour cherry (*P. cerasus*) are also possible, but fertile hybrids are only produced occasionally (Scorza and Sherman 1996).

A distinctive characteristic of peach is its self-compatible mating, unlike the majority of its congeneric species that exhibit various levels of gametophytic self-incompatibility. Selfing (Miller et al. 1989), plus important bottlenecks in its recent breeding history (Scorza et al. 1985), have resulted in a lower level of genetic variability of peach compared to the other *Prunus* crops (Byrne 1990). The high economic value of peach, its self-compatible nature that allows the development of F_2 progenies, and the possibility to shorten the juvenile period to 1–2 years after planting (Scorza and Sherman 1996) together suggest the peach can serve as an appropriate genetic and genomic reference species for *Prunus*.

A total of 42 morphological characters of simple Mendelian inheritance were discovered during the last century (Dirlewanger and Arús 2004), however until the recent development of molecular marker maps, only a few linkage relationships had been determined. Five linkage groups involving 11 major genes were reported by Monet et al. (1996).

5.2.2 Molecular Genetic Mapping in Peach

Chaparro et al. (1994) constructed the first molecular marker map in fruit trees consisting of 83 Random Amplified Polymorphic DNA (RAPD) markers, one isozyme and four morphological characters in a peach intraspecific F_2 progeny. Two more maps based on Restriction Fragment Length Polymorphism (RFLP) markers were published shortly there after; the first constructed in a peach × peach F_2 progeny (Rajapakse et al. 1995) and the second in a peach × almond F_2 progeny (Foolad et al. 1995). Later peach maps integrated dominant RAPDs

and Amplified Fragment Length Polymorphism (AFLP) markers with codominant (RFLPs) and morphological markers (Dirlewanger et al. 1998) or were constructed almost entirely with AFLPs (Lu et al. 1998). These maps were considered low level saturated maps having a low average marker density (4.5–8.5 cM/marker), and an excess of linkage groups over the eight expected based on karyotype analysis. These maps had large gaps without markers and many unlinked orphan markers (8–28%).

The first saturated linkage map, constructed exclusively with transferable markers (11 isozymes and 226 RFLPs, most of them detected with Rosaceae DNA probes) in a 'Texas' almond × 'Earlygold' peach F_2 population, was published by a European consortium (Joobeur et al. 1998). All markers were distributed into eight linkage groups with a total distance of 491 cM, representing an average density of 2.0 cM/marker, and maximal gap size of 12 cM. This map (abbreviated as the T×E map) was improved by the addition of 185 simple sequence repeat (SSR) markers, and 126 RFLPs most of them obtained with *Arabidopsis* DNA probes, and five sequence-tagged sites (Aranzana et al. 2003; Dirlewanger et al. 2004). Recently, 264 additional SSRs have been mapped to T×E using the "bin mapping" approach (Howad et al. 2005). From the 817 markers currently placed on the T×E map, 756 (92%) are based on known publicly available DNA sequences, with at least 198 (24%) of these sequences corresponding to a putative protein. Recent EST mapping has tentatively placed an additional 600 EST sequences on this map.

The *Prunus* scientific community has adopted the T×E map as the reference map for the genus. It provides a set of transferable markers that can be used as anchors for map construction in other progenies, a common linkage group terminology and marker order within each linkage group, and a highly polymorphic population that allows mapping markers that would not segregate in most peach intraspecific crosses. Table 2 presents a compilation of the inter- and intra-species peach maps that have been published. Those anchored on the *Prunus* general map are highlighted.

The network of maps interconnected with T×E reference map provides the density of markers necessary to saturate specific genomic regions of any progeny and to search genome wide for sufficient markers for quantitative trait loci (QTL) or other genetic analyses. Given that peach has a low level of intraspecific variation, a very dense "consensus" map with highly polymorphic markers well distributed in all genomic regions would insure that segregating markers are available in regions of interest in other peach crosses. To reach this goal, a supplementary effort will be required to increase the number of SSRs mapped in parallel with targeted strategies to fill regions with low SSR density (Wang et al. 2001, 2002; Georgi et al. 2002).

The existence of a single reference map has made it possible to locate the major genes and QTL that segregated in different populations (Table 3).

In total, 22 loci controlling simple characters were assigned to specific positions on the T×E map, 18 of these loci were mapped in intraspecific peach crosses and three that segregated in interspecific almond × peach crosses. For complex characters 28 QTLs for bloom and maturity time, fruit quality, tree architecture or disease resistance were also placed on the map (Abbott et al. 1998; Viruel et al. 1998; Dirlewanger et al. 1999; Etienne et al. 2002; Verde et al. 2002; Foulongne et al. 2003b).

With the current marker density, most simple characters are marked sufficiently for selection. Other strategies for gene tagging that do not require knowledge of the map position, such as bulked segregant analysis (Michelmore et al. 1991), have also been used successfully in peach (Chaparro et al. 1994; Warburton et al. 1996; Lu et al. 1998). In spite of this information being available, the use of markers for commercial breeding is still in its infancy. Marker-assisted selection is currently used in a rootstock breeding program to pyramid a root-knot nematode (*Meloidogyne* spp.) resistance gene coming from 'Nemared' peach (Lu et al. 1998; Yamamoto and Hayashi 2002; Arús et al. 2004) with another independent root-knot nematode resistance gene coming from Myrobalan plum (Claverie et al. 2004). However, selections using markers of other well-characterized genes affecting fruit characters (i.e. such as flesh color, skin pubescence, fruit shape or fruit sweetness) have not been reported. This is undoubtedly due to the fact that the variability of major traits of interest for the breeders (i.e. ripening time, fruit quality and other characters) is quantitatively inherited. There is published information on QTL characters in peach (Dirlewanger et al. 1999; Etienne et al. 2002), but a more detailed knowledge of the number, effects and map positions of the QTL affecting them is necessary before QTL associated markers can be routinely integrated in selection programs.

Table 2. Peach inter- and intra-specific maps

Population	Species	Type	Marker #	T×E Anchors	No. L.G.[1]	Total Map distance	References[2]
'Texas' 'Earlygold'	almond × peach	F_2	817	817	8	519 cM	Joobeur et al. 1998; Aranzana et al. 2003; Dirlewanger et al. 2004; Howad et al. 2005
NC174RL × 'Pillar'	peach	F_2	88	0	15	396 cM	Chaparro et al. 1994
'N J Pillar' × KV77119	peach	F_2	47	2	8	332 cM	Rajapakse et al. 1995
'Padre' × '54P455'	almond × peach	F_2	161	23	8	1,144 cM	Foolad et al. 1995; Bliss et al. 2002
'Ferjalou Jalousia®' × 'Fantasia'	peach	F_2	124	49	7	518 cM	Dirlewanger et al. 1998; Etienne et al. 2002
'Lovell' × 'Nemared'	peach	F_2	153	1	15	1,297 cM	Lu et al. 1998
'Garfi' × 'Nemared'	almond × peach	F_2	51	51	7*	474 cM	Jáuregui et al. 2001
IF7310828 × *P. ferganensis*	peach × *P. ferganensis*	BC_1	216	71	8	665 cM	Dettori et al. 2001; Verde et al. 2005
'Akame' × 'Juseitou'	peach	F_2	178	45	7*	571 cM	Yamamoto et al. 2001 and personal communication
'Summergrand' × P1908	peach × *P. davidiana*	F_2	153	57	8	874 cM	Foulongne et al. 2003a

[1] L.G. = linkage groups; *linkage groups 6 and 8 of these maps, were mapped as a single group due to the effects of a reciprocal translocation.

[2] When more than one reference is given, the data presented are either from the most recent publication or from the combination of the data from all publications.

Additional candidates for marker-assisted selection in peach are genes or QTLs that can be introgressed into peach from other wild or cultivated species, such as disease or pest resistances identified in *P. davidiana* (mildew, leaf curl, aphids, sharka) by Viruel et al. (1998) and Foulongne (2002). Introgression from wild species is facilitated with marker based whole genome selection approaches (Tanksley et al. 1989) that streamline the recovery of the genome of the cultivated species or elite genotype.

5.2.3 Comparative Mapping of Peach and Other *Prunus* Species

The transferable markers (RFLPs, SSRs and isozymes) mapped in the T×E population have been used for the construction of linkage maps in other *Prunus* species. Detailed comparisons can be made between this map and those of almond (Joobeur et al. 2000), apricot (Lambert et al. 2004), *P. davidiana* (Foulongne et al. 2003a), cherry (Dirlewanger et al. 2003) and *P. cerasifera* (E. Dirlewanger, INRA Bordeaux, 2004, personal communication). The order and distribution of the markers into the eight linkage groups was generally identical between species, suggesting a high degree of synteny. Occasional marker position discrepancies among species maps are attributed to the mapping of different duplicated loci detected by the same RFLP probe or SSR primer pair. An exception to the full collinearity observed within *Prunus* was reported by Jáuregui et al. (2001), who demonstrated the presence of a reciprocal translocation between linkage groups 6 and 8 in an F_2 progeny of 'Garfi' almond × 'Nemared' peach, and established the approximate position of the translocation breakpoint.

Taken together, these results strongly indicate that the group of *Prunus* species studied to date shares a nearly identical genome. Therefore, the information on gene sequence and position obtained in one *Prunus* species would be generally useful for the rest.

Table 3. Major genes and QTL placed on the *Prunus* reference map

Characters	L.G.[1]	Symbol[2]	Populations	References
Flesh color (white/yellow)	G1	*Y*	'Padre' × '54P455'	Warburton et al. (1996) Bliss et al. (2002)
Evergrowing	G1	*Evg*	'Empress op op dwarf' × PI442380	Wang et al. (2002)
Internode length	G1	QTL	(*P. ferganensis* × 'IF310828')BC1	Verde et al. (2002)
Powdery mildew resistance	G1	QTL	'Summergrand' × P1908	Foulongne et al. (2003b)
Flower color	G1	*B*	'Garfi' × 'Nemared'	Jauregui (1998)
Root-knot nematode resistance	G2		'P.2175' × 'GN22', 'Akame' × 'Juseitou'	Claverie et al. (2004), Yamamoto et al. (2001)
		Mi[3]	'Lowell' × 'Nemared', 'Garfi' × 'Nemared' 'Padre' × '54P455'	Lu et al. (1998), Bliss et al. (2002) Jáuregui (1998)
Ripening time, fruit skin color, soluble-solids content	G2	QTL	(*P. ferganensis* × 'IF310828')BC1	Verde et al. (2002)
Double flower	G2	*Dl*	'NC174RL' × 'PI'	Chaparro et al. (1994)
Broomy (or pillar) growth habit	G2	*Br*	Various progenies	Scorza et al. (2002)
Flesh color around the stone	G3	*Cs*	'Akame' × 'Jusetou'	Yamamoto et al. (2001)
Anther color (yellow/anthocyanic)	G3	*Ag*	'Texas' × 'Earlygold'	Joobeur (1998)
Leaf curl resistance	G3	QTL	'Summergrand' × P1908	Viruel et al. (1998)
Fruit weight, fruit diameter, glucose content	G3	QTL	'Suncrest' × 'Bailey'	Abbott et al. (1998)
Polycarpel	G3	*Pcp*	'Padre' × '54P455'	Bliss et al. (2002)
Flower color	G3	*Fc*	'Akame' × 'Jusetou'	Yamamoto et al. (2001)
Blooming time, ripening time, fruit development period	G4	QTL	'Ferjalou Jalousia®' × 'Fantasia'; (*P. ferganensis* × 'IF310828')BC1	Etienne et al. (2002) Verde et al. (2002)
Soluble-solids content, fructose, glucose	G4	QTL	'Ferjalou Jalousia®' × 'Fantasia'	Etienne et al. (2002)
	G4	*F*	(*P. ferganensis* × 'IF310828')BC1;	Verde et al. (2002), Dettori et al. (2001)
Flesh adhesion (clingstone/freestone)			'Akame' × 'Juseitou'	Yamamoto et al. (2001)
Flesh texture (melting/non-melting)	G4	*M*	'Dr. Davis' × 'Georgia Belle' and 'Georgia Belle'⊗	Peace et al. (2005)
	G5	*D*	'Ferjalou Jalousia®' × 'Fantasia'	Dirlewanger et al. (1998, 1999)
Non-acid fruit				Etienne et al. (2002)
Sucrose, malate, titrable acidity, pH, sucrose	G5	QTL	'Ferjalou Jalousia®' × 'Fantasia'	Etienne et al. (2002)
Skin hairiness (nectarine/peach)	G5	*G*	'Ferjalou Jalousia®' × 'Fantasia'; 'Padre' × '54P455'	Dirlewanger et al. (1998, 1999) Bliss et al. (2002)
Kernel taste (bitter/sweet)	G5	*Sk*	'Padre' × '54P455'	Bliss et al. (2002)
Ripening time, fruit skin color, soluble-solids content	G6	QTL	(*P. ferganensis* × 'IF310828')BC1	Verde et al. (2002)
Plant height (normal/dwarf)	G6	*Dw*	'Akame' × 'Juseitou'	Yamamoto et al. (2001)
Leaf shape (narrow/wide)	G6	*Nl*	'Akame' × 'Juseitou'	Yamamoto et al. (2001)
Male sterility	G6	*Ps*	'Ferjalou Jalousia®' × 'Fantasia'	Dirlewanger et al. (1998)
Powdery mildew resistance	G6	QTL	'Summergrand' × P1908	Foulongne et al. (2003b)
Leaf curl resistance	G6	QTL	'Summergrand' × P1908	Viruel et al. (1998)
Fruit shape (flat/round)	G6	*S**	'Ferjalou Jalousia®' × 'Fantasia'	Dirlewanger et al. (1998, 1999)

[1] L.G. = Linkage group; G6-G8 genes located close to the translocation breakpoint between these two linkage groups.
[2] QTL are included if they have been consistently found (at least in two independent measurements) in the indicated populations.
[3] One or two genes of nematode resistance with different notations and one QTL with have been described in this linkage group.

Table 3. (continued)

Characters	L.G.[1]	Symbol[2]	Populations	References
Leaf color (red/yellow)	G6–G8	*Gr*	'Garfi' × 'Nemared'; 'Akame' × 'Juseitou'	Jauregui (1998) Yamamoto et al. (2001)
Fruit skin color	G6–G8	*Sc*	'Akame' × 'Juseitou'	Yamamoto et al. (2001)
Leaf gland (reniform/globose/eglandular)	G7	*E*	(*P. ferganensis* × 'IF310828')BC1	Dettori et al. (2001)
Resistance to mildew	G7	QTL	(*P. ferganensis* × 'IF310828')BC1	Verde et al. (2002)
Powdery mildew resistance	G8	QTL	'Summergrand' × P1908	Foulongne et al. (2003b)
Quinase	G8	QTL	'Ferjalou Jalousia®' × 'Fantasia'	Etienne et al. (2002)

5.2.4 Comparative Mapping of Peach to *Arabidopsis*

In order to examine the evolution of the plant genome, it is extremely valuable to compare structural organization of relatively similar sized genomes of plants that have diverged over significant evolutionary time. Thus, identification of significantly conserved regions potentially identifies functional chromosomal units. The *Prunus* map and the *A. thaliana* genome sequence have been compared using a set of RFLP markers mapped in T×E obtained either with probes of different species (mainly *Prunus* and apple) that had a high level of sequence conservation with *Arabidopsis* (TBLASTX values lower than 10^{-15}) or with *Arabidopsis* probes that hybridized well to *Prunus* DNA (Dominguez et al. 2003). The position of 227 *Prunus* loci (map average density of 2.6 cM/marker) could be compared to that of 703 *Arabidopsis* homologous sequences. The criterion for declaring a syntenic region was that three or more homologous markers had to be located within 1% of the *Prunus* map distance (6 cM) and within a 1% of the *Arabidopsis* genome (1.2 Mb). In addition, blocks with gaps longer than 1% of either genome were rejected. With these stringent criteria it was possible to detect 37 syntenic regions, covering 23% and 17% of the *Prunus* and *Arabidopsis* genomes, respectively. The longest of these regions included 13 markers for a distance of 25 cM in linkage group 2 of *Prunus* and 16 homologous sequences spanning 5.4 Mb in chromosome 5 of *Arabidopsis*.

Similarly, higher resolution studies have not supported extensive preservation of localized genome structure between the two genomes. The sequence of peach bacterial artificial chromosomes (BACs) and BAC ends located in several locations in the peach genome was compared with that of *Arabidopsis*. (Georgi et al. 2003; Sook Jung, personal communication). Predicted genes in these sequences were homologous to genes scattered along the five chromosomes of *Arabidopsis*, with an approximate preservation limit of 2 genes. In summary, macro- and microsynteny results concur in detecting a fragmentary preservation between these two genomes putatively separated for more than 90 million years.

5.3 Genomics

5.3.1 Construction of the Peach Physical Map and its Use in Gene Discovery

5.3.1.1 Structural Genomics in Peach

Large-insert libraries and physical maps are important tools for map-based cloning of Mendelian loci (Arondel et al. 1992) and QTL (Frary et al. 2000). In peach BAC libraries were constructed for 'Nemared' rootstock and a haploid of 'Lovell'. The restriction enzymes used were *Hind*III and *Sau*3A1, respectively. The 'Nemared' library consists of approximately 40,000 clones with average inserts approximately 60 kb in size. The theoretical coverage of the genome is 8–10 fold but in practice it is approximately 4–5 fold. The haploid Lovell library consists of approximately 35,000 clones with an approximate average insert size around 80 kb yielding a theoretical twelve fold coverage of the genome.

Utilizing these BAC library resources the International Rosaceae Genome Consortium (IRGC) is constructing a complete physical map of the peach genome anchored on the general *Prunus* genetic

Table 4. Current summary data for the peach physical map

Number of clones fingerprinted	21,120
Number of clones used for map contig assembly	18,387
Number of singletons	7,194
Number of clones in contigs	11,193
Number of contigs	1,367
Size of contigs: >200 (chloroplast genome)	1
51–100 clones	1
26–50 clones	27
10–25 clones	3,478
3–9 clones	763
2 clones	228
Number of anchored contigs	149 (2,031 clones)
Physical length of contigs	210–230 Mb
Physical length of the anchored contigs	33 Mb

map (Joobeur et al. 1998) essentially following strategies utilized to develop the *Drosophila* physical map and others (Marra et al. 1999; Hoskins et al. 2000; Tao et al. 2001; Cone et al. 2002). The approach utilizes a combination of hybridizing mapped markers, BAC fingerprinting and in our case hybridizing expressed sequence tag (EST) sequences. With the current *Prunus* molecular marker map resources, 210 low-copy mapped RFLP markers, 4,000 peach fruit ESTs, 80 resistance gene analogs, 200 specific complimentary DNAs (cDNAs) and numerous specific AFLP markers have been hybridized to the BAC libraries. We completed BAC fingerprinting approximately 25,000 BACs (15,000 from the 'Nemared' library and 5,000 from the haploid 'Lovell' library from which approximately 15,000 have been used to construct an initial physical map (see map specifics in Table 4 and www.genome.clemson.edu/gdr/).

FPC (V4.7) (Soderlund et al. 2000) was used to construct an initial physical map of the peach genome following strategies employed to construct physical maps in other crops (Marra et al. 1999; Tao et al. 2001). Initially, the map was constructed at a cut-off from e^{-10} to e^{-12} and tolerance 5 to obtain all high confidence overlapping BAC inserts (contigs). These were then merged by testing end clones at cut-off values ranging e^{-8} – e^{11}. As there was a significant amount of hybridization data, merges were often achieved based on common hybridization of BACs in different contigs. However, if only BAC fingerprint data existed, we noted the merge points for further testing. Presently, the framework map is composed of ~1,000 contigs containing approximately 11,000 clones (see Table 4). Based on estimates of an average BAC insert size of 60 kb and an average of 60% degree of overlap in contigs, 80% or better of the peach genome should be high confidence contigs. Currently we are adding in orphan singleton BACs (approximately 7,000 not in contigs from initial map construction) and merging contigs at lower cutoff scores is underway to finalize the initial peach physical map. Preliminary estimates from trial merges of contigs suggests that the initial map will consist of 800–900 contigs with an average of 12 clones/contig upon completion of the analysis. Since the map includes marker hybridization data from the general *Prunus* genetic map, the developing physical map is directly anchored to the genetic map. From initial analysis of the integrated genetic/physical map, there is already evidence for duplication of some regions of the peach genome. The developing physical map is located at the *Prunus* genome website within the Genome Database for Rosaceae (GDR) at Clemson University www.genome.clemson.edu/gdr/. This database is under ongoing development (for details see below).

5.3.2 Functional Genomics

5.3.2.1 Peach EST Functional Genomics Database Development

With the support of the United States Department of Agriculture, the IRGC initiated a peach EST project with the central goal of developing the unique expressed gene set (unigene set) for peach. The cur-

rent efforts are centered on sequencing 30,000–40,000 cDNAs from libraries of developing fruit, shoot and seeds. Original expectations were that these would resolve into 3,000–4,000 unigenes, however, this number was obtained from the first 15,000 sequences finished. The data summary for the completed analysis of 23,000 cDNAs from developing peach fruit and almond seed libraries is available at the website www.genome.clemson.edu/gdr/. Sequencing of developing shoot and root cDNAs is in progress.

We have also begun mapping peach ESTs on the developing physical/genetic peach map and have determined that a significant portion of ESTs (11%) hybridized on our BAC libraries are placed directly on genetically mapped anchored contigs in the physical map. From the current 15,000 sequences, a peach/almond unigene set has been initiated. This unigene set consists of 3,842 putative unique genes.

5.3.2.2 Transcript Map

A set of 180 ESTs (11%) have been localized in 86 locations (involving 80 core markers) on the general *Prunus* genetic map by common hybridization with RFLP markers to BACs in the 'Nemared' library. This EST resource will provide candidate genes for marked regions of the *Prunus* maps containing traits of interest and will be available on-line through the *Prunus* genome database noted above. From the initial fruit unigene set, we have completed hybridizing in excess of 4,000 ESTs onto the 'Nemared' BAC library. From this set, 184 ESTs have been directly located on the general *Prunus* genome map through common hybridization of mapped molecular markers and ESTs. BACs have been identified in the 'Nemared' library for nearly 85% of these ESTs. Initial hybridizations of $\sim$ 100 ESTs, that failed to detect BACs in the 'Nemared' library, on the haploid 'Lovell' BAC library have been 60% successful. Thus, upon completion of the physical map, virtually all unigene EST locations will be identified.

We are also mapping resistance gene analogues (RGAs) and resistance associated genes (RAGs). We have completed hybridizing over 80 different RGA/RAG genes. From these analyses, we have positioned on the general *Prunus* map/physical map approximately 40 RGAs and RAGs placing a number of these genes in regions known to contain resistance to powdery mildew, plum pox virus and parasitic nematodes (Lalli et al. 2005). This map serves as an initial starting point in the identification and marking of important disease resistance genes in peach and other *Prunus* species.

The structural and functional genomics databases of peach serve as tools for microsynteny analysis of regions of interest and for gene cloning investigations. With the integration of sequenced cDNA loci (EST loci), the physical map database immediately provides candidate genes located in the genetically marked intervals containing traits of interest. These associations provide the potential to greatly speed the process of gene discovery and characterization.

5.3.3 Comparative Physical Mapping of Peach and Other Model Genome Species

One of the most important contributions of DNA marker technology to fundamental studies in plant biology is the ability to rapidly compare genome organization in closely related as well as diverse species. Comparative mapping studies can identify highly conserved genome blocks, and regions of lesser conservation. Identification and molecular dissection of these evolutionarily conserved regions may uncover genetic associations that by virtue of their preservation, are implicated as important for plant development. In addition, comparative mapping information can serve as a starting point for initial mapping and gene cloning investigations in poorly characterized species.

The comparative genome sequence organization of plant genomes has not been examined as extensively as chromosomal mapping level studies, however, some reports suggest that within families, there is a significant preservation of gene repertoire and order among plants with quite different genome sizes (Dunford et al. 1995; Bennetzen et al. 1996; Chen et al. 1997; Kilian et al. 1997; Aramova et al. 1998). Initial comparative sequencing studies between *Arabidopsis* and rice have revealed some conservation of genomic structure in defined regions. The data suggests, however, that genes are being dispersed into and out of regions by mechanisms such as transposition, thus, obscuring microsynteny across great evolutionary distances (Van Dodeweerd et al. 1999). Future research is necessary to examine the degree of microsynteny within and among plant families.

As discussed in the genetic mapping section above, limited comparative mapping between peach and other model genome species was done utilizing molecular marker technologies (Dominguez et al. 2003). This lack of comparative data is also evident at

the high-resolution level, however, there are several reports suggesting that specific regions of the peach genome maintain a very limited microsynteny with the *Arabidopsis* genome (Georgi et al. 2002). These initial studies demonstrate that substantial genome rearrangements have occurred thus limiting the value of interfamily comparative genomics as a tool for gene discovery. However, within *Prunus*, the high level of genome preservation at the low-resolution scale suggests that utilization of the peach genome as an anchor for identification of important genes in other species is more promising. Initial high-resolution comparative studies of peach with plum and apricot suggest that the peach genome database will serve as an excellent source of candidate genes for traits in these species (D. Esmenjaud, INRA Antibes, France 2004, personal communication; M.Badenes, IVIA, Valencia Spain, 2004, personal communication).

5.4 Peach Tissue Culture and Transformation

Genetic transformation is a complementary method of stone fruit improvement that may be particularly useful to increase biotic and abiotic stress resistance and fruit quality (Scorza 1991, 2001; Scorza et al. 1995a; Srinivasan et al. 2004). Plant genetic transformation generally involves the transfer of DNA with the desired gene(s) into cells, and the regeneration of transgenic plants from the transformed cells through in vitro culture.

While genetic transformation is an important tool for peach improvement, a reliable and reproducible transformation and regeneration system from somatic tissue has yet to be developed. The following summarizes the reports of work in peach transformation and regeneration.

Although induction of somatic embryogenesis has been reported for peach, conversion of these somatic embryos into plants is far from routine (Scorza 2001). Raj Bhansali et al. (1990) induced somatic embryos from 1–3 mm long immature zygotic embryos of peaches and nectarines. Guohua and Yu (2002) produced embryogenic callus from immature cotyledons of four Chinese peach cultivars using a two-step process that induced up to 95% of the immature embryos to produce callus with up to eight somatic embryos per explant. Up to 75% of these somatic embryos produced shoots. Scorza et al. (1990a) produced somatic embryogenic cultures from immature (45–50 days post bloom) embryos. Following a 6-month culture period on the media of Hammerschlag et al. (1985) these cultures became growth regulator independent (habituated) and continually produced somatic embryos for up to four years. These embryogenic cultures only rarely germinated to produce viable shoots even when exposed to a number of treatments including cold treatment and various growth regulators.

Direct adventitious shoot regeneration without intervening somatic embryo production has been induced from callus derived from immature zygotic peach embryos (Hammerschlag et al. 1985). The use of immature zygotic explants limit source material availability to only a few months out of the year. Pooler and Scorza (1995) demonstrated adventitious shoot production from mature cotyledons of peach rootstock ('Nemaguard', 'Flordaguard', and 'Nemared') seeds that had been cold-stored at 4 °C for 1–3 years.

As with all peach regeneration systems developed to date successful regeneration is highly genotype dependent. Most of the preceding reports of regeneration from peach have focused on the use of zygotic tissues, and most from immature zygotic embryos. In contrast, Gentile et al. (2002) reported adventitious shoot regeneration from callus cultures of young leaves (1–2 mm long) from in vitro-grown peach shoots in a medium containing 9 μM BA and 0.54 μM NAA. Regeneration rates of 13–28% were obtained using three cultivars from diverse origins and two seedling selections. Most regeneration was obtained from leaf petioles.

Clearly, it is possible to regenerate peach plants in vitro. This has been achieved for the most part by using zygotic tissues. These explant sources have generally not been favored for tree fruit transformation because the ability to improve established cultivars is lost. Each seed-derived genotype is unique and not a clone of the parent. Transformation of zygotic tissues would be useful for providing unique and useful genes to breeding programs where they could be incorporated into new germplasm. Given the facts that the generation cycle for peach is approximately three years [a short cycle when compared with most tree fruit species (Sherman and Lyrene 1983)]; that most new peach cultivars are produced by breeding programs versus the selection of sports of established cultivars; and that peach varieties are continually replaced at a fairly rapid pace (10–12 years or less in some areas), the efficient transformation of peach

germplasm can be of great benefit to the genetic improvement of this species.

While the production of transgenic *Prunus* depends largely on the efficiency of regeneration of plants from transformed cells, the efficiency of transformation itself is also an important factor, one that takes on an even greater level of importance in the case of low regeneration rates. Several reviews have been published on transformation of *Prunus* species, including peach (Scorza and Hammerschlag 1992; Scorza et al. 1995a; Rugini and Gutierrez-Pesce 1999; Srinivasan and Scorza 1999, 2004). Transformation efficiency is affected by many factors including the method of transformation (e.g., *A. tumefaciens* or biolostics); transformation environment; and the antibiotic selection pressure. In most published reports, *A. tumefaciens* has been used to transfer the DNA plasmids carrying the gene(s) of interest to peach cells. Neomycin phosphotransferase (NPTII) has been used as the selectable marker, and in some cases, β-glucuronidase (GUS) or green fluorescent protein (GFP) as a visual marker of transformation (Pérez-Clemente et al. 2004; Padilla et al. 2006).

Although peach is infected by wild *A. tumefaciens* and crown gall disease is common in *Prunus* (Scorza and Sherman 1996), transformation efficiency of peach cells in vitro with disarmed *A. tumefaciens* appears to be relatively low (Padilla et al. 2006). Scorza et al. (1990b) reported the transformation of peach leaf segments, immature embryos, and long-term embryonic callus using *A. tumefaciens* strain A281 carrying plasmid pGA472 with the NPTII selectable marker. Transformation rates of 5% of immature embryos and up to 64% of leaf segments were observed. These explant sources did not undergo organogensis, thus no transgenic shoots were obtained from this work.

In addition to *A. tumefaciens*-based transformation particle bombardment (biolistics) has also been used to produce stably transformed embryogenic peach callus (Ye et al. 1994). Embryogenic callus derived from immature embryos was used as the starting material. No regeneration was obtained from the transformed embryogenic callus produced in this study. Transient expression tests of biolistic transformation of embryogenic callus, embryonic axes, cotyledons, and immature embryos demonstrated high levels of transformation efficiency. The ability to transform these explants was considered to be significant because regeneration from these tissues had been previously reported.

To date, there are only two reports of the development of transgenic peach plants. Smigocki and Hammerschlag (1991) regenerated transgenic peach plants from immataure zygotic embryos following transformation with a shooty mutant strain of *A. tumefaciens*, *tms*328::Tn5, which carried an octopine type Ti plasmid with a functional cytokinin gene and a mutated auxin gene. The use of this cytokinin-producing shooty-mutant strain of *A. tumefaciens* may have been responsible for the successful regeneration of transformed shoots and also for the altered growth habit of the transgenic trees (Hammerschlag et al. 1997). Pérez-Clemente et al. (2004) developed several transgenic peach plants by using zygotic embryo explants from stored seed. Efficiency of plant production was reported as 3.6 + 1.0%. In both reports of peach transformation few transgenic plants were produced and an efficient, reproducible transformation system remains to be developed.

Peach is not unique in the *Prunus* in its recalcitrance to transformation and regeneration. There are few reports of the successful production of transgenic *Prunus* species. Those species that have been transformed include apricot (*P. armeniaca*) (Laimer da Camara Machado et al. 1992), sweet cherry (*P. avium*) (Brasileiro et al. 1991), sweet × sour cherry (Dolgov and Firsov 1999), almond (*P. amygdalus*) (Miguel and Oliveira 1999) *P. avium* × *P. pseudocerasus* cv. Colt (Gutierrez-Pesce et al. 1998), *P. subhirtella autumno rosa* (da Camara Machado et al. 1995) and *P. domestica* (European or prune plum) (Mante et al. 1991; Padilla et al 2003). For most of these species there exists a single report of the development of only a few transgenic plants. Although the *P. domestica* system, uses mature seeds as the explant source and therefore is not a clonal system it has been used repeatedly to develop transgenic trees (Mante et al. 1991; Scorza et al. 1994, 1995b; Padilla et al. 2003) and presents what can be considered a reliable and routine system. It is such a system in terms of reliability and productivity that remains a goal for peach and one that will advance the utilization of gene transfer for peach improvement.

5.5 Future Directions

Significant progress has been made in recent years to understand the genome organization in peach and the other closely related species in Rosaceae. For

Prunus species, the genome organization is highly collinear and thus genetic resources developed in one key species will serve as a tool for identification, characterization and manipulation of important trait controlling genes in the other species. In this regard, genomic research in peach has significantly progressed toward the completion of a physical map/genetic map resource in peach with significant numbers of genes identified and mapped through EST and genomic sequencing efforts. This information is publicly available in the GDR. Recent reports utilizing these resources have demonstrated the importance of this database for identification and study of important fruit tree genes. Manipulation of these genes in peach awaits the development of a reliable transformation system for peach, however, recent reports (Perez-Clemente et al. 2005) suggest that this lies just around the corner and transformation in companion species such as *Prunus domestica* is routine.

Future work in peach will focus on the utilization of this gene information and marker systems for manipulation of important characters in the breeding schemes. The integration of the molecular genetic resources for peach with the traditional breeding programs promises to streamline the breeding process and provide new and improved varieties for the global market. Additionally, significant research efforts remain particularly in the characterization of many of the fundamental gene systems responsible for the unique and important life history traits of these fruit tree species, such as, endodormancy, cold hardiness, chilling requirements for flower bud break, growth habit and drupe fruit development. Other targets of research in peach should include the technologies of proteomics and metabolomics both areas that promise to provide much needed information the genetic control of important fruit quality characters as well as fundamental knowledge on the genetic basis of fruit tree physiology.

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