Chapter 11
Plums

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Abstract Most of the plums grown commercially are either the hexaploid, *Prunus domestica* (European) or the diploid, *P. salicina* (Asian or Japanese). Common goals of European plum breeders are cold hardiness, modest tree size, self fertility and productivity. Some of the key abiotic problems confronting Japanese plum production are susceptibility to spring frosts, insufficient winter hardiness and limited soil adaptations. Fruit quality and disease resistance are important goals in all plum breeding projects. The genetics of only a few traits have been investigated in plum; however, significant progress has been made in identifying horticulturally useful germplasm. A Myrobalan plum clone was crossed with an almond-peach hybrid to generate a microsatellite genetic linkage map and a resistance gene to the root knot nematode (*Ma*) was identified. A transgenic European plum clone was produced that carries the plum pox virus coat protein gene (PPV-CP) and has strong resistance to all four major serotypes of PPV.

11.1 Introduction

Plums contain a hard pit, and thus are classified with other stone fruits in the genus *Prunus* of the Rosaceae. Most of the plums grown commercially fall into one of two groups: European (hexaploid) or Japanese (diploid) types (Fig. 11.1). European plums (primarily *Prunus domestica*) are generally better adapted to cooler regions than Japanese types.

Within *P. domestica*, several groups of cultivars are recognized such as Green Gage (or Reine Claude) types and prunes. The *insititia* subspecies of *P. domestica* includes bullaces, damsons, mirabelles and St. Julien types. The greengage, mirabelle and damson plums are used a great deal in the food processing industry. They are processed into jams, jellies, canned fruit, juices (prune juice, for example), and alcoholic drinks such as brandies and cordials. European plums with a sugar content high enough so that they can be dried with the pit intact are referred to as

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Fig. 11.1 Bearing habit of a typical Japanese-type shipping plum

prunes. In some countries the term ‘prune’ refers primarily to the dried product; elsewhere the term refers to the fresh fruit as well. Nearly all prune production in California, and much of the world, is of ‘French Prune’ and its clones, under such names as ‘Prune D’Agen’, ‘Petite Prune’ and ‘Prune D’Ente’.

Leading countries in European plum production are the former U.S.S.R., Romania, Yugoslavia, Germany, United States and Hungary. Part of this production is processed into dried fruit. Production of prunes is concentrated in the United States, primarily California, followed by France, Yugoslavia, Chile and Argentina. In California there are nearly 35,000 hectares of prunes concentrated in the Sacramento, Santa Clara, Sonoma, Napa and San Joaquin Valleys. Currently, these farms produce more than twice as many dried plums as the rest of the world combined; about 99% of the U.S.A. supply and 70% of the world supply. Lesser amounts of European plums are grown in Idaho, Washington, Oregon, Michigan, and New York for both fresh and canned use.

The term ‘Japanese plum’ originally was applied to *Prunus salicina* (formerly *P. triflora*), but now includes all the fresh-market plums developed by intercrossing various diploid species with the original species. These plums were initially improved in Japan and later, to a much greater extent, in the United States. Most of these plums are consumed as fresh fruit and in many areas of the world these are the predominant plum found in the grocery store. A wide array of skin and flesh colors are available (Fig. 11.2), but in recent years the market has been dominated by black skin with light yellow or red flesh. Production of Japanese plums is led by China, followed by the United States. Production in the United States is concentrated in

Fig. 11.2 Range in fruit color and size for diploid plum species and breeding lines

California. Substantial production also comes from Mexico, Italy, Spain, Chile, Pakistan, Republic of Korea, Egypt, Australia, South Africa, and Argentina. Production of Japanese plums has been increasing in Europe and Asia. Although most U.S. Japanese plum production is in California, Japanese plums are grown in small quantities in many states of the U.S.A.

11.2 Evolutionary Biology and Germplasm Resources

Within Rosaceae, the sub-family Prunoideae is distinguished by having simple leaves and a 1- carpelled, drupaceous fruit with a deciduous calyx. Plums are separated from cherries by lack of a terminal bud, presence of a suture and a waxy bloom on the fruit, and a flatter pit. Plums are placed in the Prunophora sub-genus to separate them from peaches, almonds and cherries based on having sutured fruit with a waxy bloom, solitary axillary buds, and no terminal buds. Peaches and almonds differ in having three axillary buds with usually sessile, solitary flowers, and conduplicate (rolled) leaves in a terminal bud. Within Prunophora, section Euprunus contains the Asian and European species of plums, distinguished by 1–2 flowers per bud, stone often sculptured, and leaves rolled in the bud. Section Prunocerasus contains the American plum species, that have three or more flowers per bud, smooth stone and leaves folded in the bud. However, Asian species appear to fit better in Prunocerasus both taxonomically and horticulturally. In the real world, these characteristics are not definitive, there being exceptions to most of them.

There are 20–40 plum species depending on authority, many of which intergrade from one to another in the wild (Table 11.1). There are three independently

Table 11.1 Important sources of germplasm in plum breeding (2x = 2*n* = 16)

Species	Chromosome number	Location+	Useful characters
P. allegehaniensis Porter	16	Conn. To Penn.	Resistance to crown gall
P. americana Marsh.	16	Eastern U.S.A. to Rocky Mountains	Tough skin; very winter hardy
P. angustifolia Marsh.	16	New Jersey to Florida, west to Illinois and Texas	Resistance to bacterial leaf spot; limited tolerance to plum leaf scald
P. besseyi Bailey	16	Manitoba to Wyoming, south to Kansas and Colorado	Late bloom; high heat threshold; very winter hardy; resistant to crown gall
P. cerasifera Ehrh.	16 (24,32,48)	Western Asia, Caucasus, Balkan	Earliness; nematode resistance
P. domestica L.	48	Europe	High flavor and fruit quality
P. hortulana Bailey	16	Midwest and S.E. U.S.A.	Resistance to bacterial leaf spot
P. maritima Marsh.	16	Maine to Virginia	Late bloom; high heat threshold
P. mexicana S.Wats.		Southern U.S.A. to Texas	Large tree; low suckering
P.munsoniana Wight & Hedr.	16	Midwest U.S.A.	Good fruit; productive
P. nigra Ait.	16	New Brunswick to Assiniboine Mts, south to New York, Ohio and Wisconsin	Very winter hardy
P. salicina Lindl.	16 (32)	China	Good size, color and attractiveness; exceptional firmness and keeping quality at high temperatures; very winter hardy
P. simonii Carr.	16	China	Firmness; upright tree
P. spinosa L.	32	Europe	Disease resistance
P. subcordata Benth.	16	California, Oregon	Drought tolerance; high chill requirement
P. umbellata Ell.	16	North Carolina to Florida, Alabama, Mississippi and Texas	Resistance to crown gall

Source: Okie and Weinberger 1996, Ramming and Cociu 1991 domesticated groups of plums. The hexaploid ($2n = 6x = 48$) European plum, *P. domestica*, is the most commonly grown species in cooler regions. The diploid ($2n = 2x = 16$) Asian or Japanese plum, *P. salicina*, originated in China. The North American plums, such as *P. americana*, *P. angustifolia*, *P. maritima* and *P. subcordata*, were grown at a number of locations across the U.S.A. and Canada by native peoples and early Americans (Fig. 11.3).

The European plum, *P. domestica,* represents all the hexaploid plums, including those formerly classified as *P. insititia* but now given subspecies rank. That subspecies is characterized by a smaller tree, smaller leaf, and smaller fruit that is generally processed in some way rather than eaten fresh. Crane and Lawrence (1956) thought *P. domestica* originated in Asia Minor as a triploid hybrid between *P. cerasifera* (Myrobalan plum) and the tetraploid *P. spinosa* L., which then doubled to produce a fertile hexaploid. Newer cytological work, indictes that *P. spinosa* itself carries the genome from *P. cerasifera* plus a second one from an unknown ancestor (Reynders-Aloisi and Grellet 1994). Thus, *P. domestica* may be descended from polyploid forms of *P. cerasifera*, which has a long history of local use and selection across the continent, and has a range of fruit color and palatability.

Fresh and dried fruit of *Prunus cerasifera* have been used for centuries in West Asia from the Tien Shan and Pamir mountains over to the Caucasus Mountains. Many local cultivars have been selected for fruit. Myrobalan is also widely used worldwide as a rootstock for plum. Yoshida suggests *P. cerasifera* is the progenitor of all plum species, because of its native range, and cross- and graft-compatibility with many other species (Okie and Weinberger 1996).

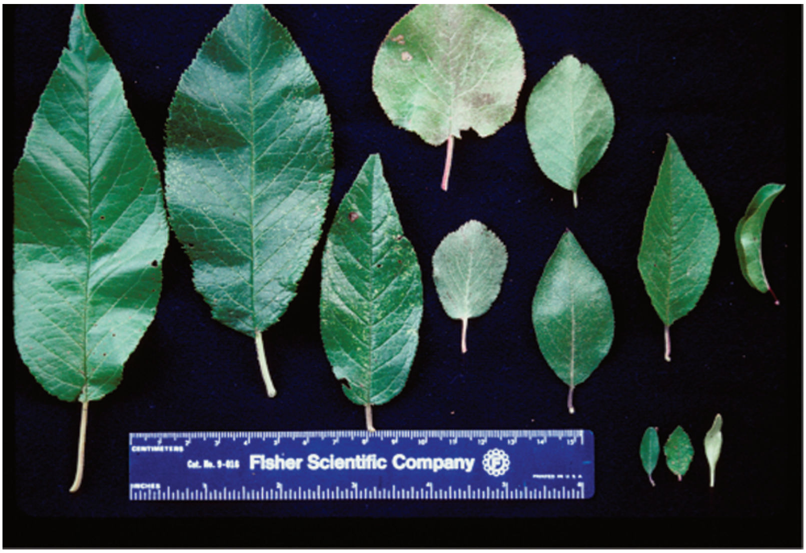

Fig. 11.3 Range in leaf shape and size for North American plum species

Although sometimes used for drying and processing, most wild *P. spinosa* fruit are bitter. This species ranges from Scandinavia across Europe to Asia Minor. In Soviet Georgia, natural *P. spinosa* have been found with $2n = 16$, 32, 48, 64 or 96. Natural hybrids ($2n = 48$) between *P. cerasifera* and *P. spinosa* have also been found.

Low-chilling types of the Japanese plum, *P. salicina,* are located in southern China and Taiwan. Cold-hardy plums in northern China have been classified as *P. ussuriensis* and *P. gymnodonta*, but are otherwise very similar to *P. salicina*. Modern breeding programs, especially in the areas of the former U.S.S.R., have utilized this source of hardiness. Western taxonomists have described other Chinese species such as *P. thibetica*, and *P. consociiflora*, but these are not listed in Chinese taxonomic references as distinct species and probably represent variants within *P. salicina*. *Prunus simonii* was described by Western botanists based on cultivated specimens. This species (probably the same clone each time) was used in developing California cultivars because of its firm flesh and strong flavor. Chinese botanists describe it as native to north China, and occasionally cultivated. It has some characters reminiscent of apricot and was thought by some to have descended from a natural hybrid, but more likely is just an upright variant of *P. salicina* (Okie and Weinberger 1996).

Collections of plum germplasm consist primarily of local selections and cultivars, plus a small amount of wild accessions. Because most plum breeding programs are for cultivar development and use primarily adapted, improved parents, there is little systematic evaluation of the wild germplasm. A major collection of *P. salicina* is at the Research Institute of Pomology, Chinese Academy of Agricultural Sciences, Xingcheng, Liaoning, China. Several European research institutions have large collections of European plums, including the Institute of Plant Genetics and Crop Plant Research Fruit Genebank, Dresden, Germany and the Swedish University of Agricultural Sciences, Balgard Department of Horticultural Plant Breeding, Kristianstad, Sweden. Large collections of both diploid and hexaploid plums are found at the Institut National de la Recherche Agronomique, Bordeaux and Avignon, France as well as at the United States Department of Agriculture – Agricultural Research Service, National Clonal Germplasm Repository, Davis, California, U.S.A. Unfortunately, most of the wild plum species and relatives are poorly represented in these collections.

11.3 History of Improvement

European plums have been a commonly grown garden tree in Europe since the first century A.D. Several cultivars known in 1597 are still grown, such as ‘Reine Claude’. One of the earliest plum breeders was Thomas Andrew Knight in England, whose work encouraged nurseryman Thomas Rivers who released ‘Early Rivers’ in 1834, followed by ‘Early Transparent Gage’, ‘Czar’, ‘Monarch’ and ‘President’. By the early 1900s, plum breeding was being carried out at Long Ashton (later East Malling) and John Innes research stations (Roach 1985). In other European countries, local selections of the older cultivars were made and became established, but little formal breeding was done until later. In Eastern Europe, intentional breeding goes back over 50 years, with many cultivars released.

Early settlers to North America brought European plums with them, but the plums thrived only in more northern areas. A few selections were made from this germplasm base, although improvements were minor. Luther Burbank developed cultivars of European plums, but only ‘Giant’, ‘Sugar’ and ‘Standard’ became important commercially. The first public breeding program for European plums was established at Geneva, New York in 1893. This program released ‘Stanley’ in 1926, which is still important in many countries. Breeding began at Vineland, Ontario in 1913 and they have released numerous fresh market cultivars adapted to northern North America, including ‘Valor’ (1967), ‘Verity’ (1967), ‘Vision’ (1967), ‘Veeblue’ (1984) and ‘Voyageur’ (1987), all of which are commercially planted in Ontario.

Stones from plums have been found in Japan dating back to the Yayoi Era, about 2,300 years ago. Japanese books that are 1,500 years old mention cultivated plums. Plums have been common garden plants in Japan for centuries, but improvement efforts have only occurred in the last century. Plum culture in Japan and also Korea is so ancient that it is not possible to tell if the countries were ever part of the native range for plums. Trees of improved *P. salicina* cultivars ‘Kelsey’ and ‘Abundance’ were introduced into the United States from Japan over 100 years ago. Luther Burbank intercrossed these and other imports with *P. simonii* and North American species, resulting in ‘Beauty’, ‘Burbank’, ‘Duarte’, ‘Eldorado’, ‘Formosa’, ‘Gaviota’, ‘Santa Rosa’, ‘Satsuma’, ‘Shiro’, and ‘Wickson’. These plums formed the basis for the world’s shipping plum industry, and some are still widely grown. Pure *P. salicina* and related species have been little used as parents since Burbank’s early hybridizations and few pure *P. salicina* clones are available outside of China. Most of Burbank’s plums are thought to have descended from *P. salicina*, *P. simonii* and *P. americana*. In general, *P. salicina* contributed size, flavor, color and keeping ability; *P. simonii* contributed firmness and acidity; whereas the American species gave disease resistance, tough skin and aromatic quality. Burbank was fortunate in having improved native material available to supply these characters (Okie and Weinberger 1996).

With the advent of Burbank’s improved plums that were large and firm enough to ship long distances, a new industry developed in California that caused industries in other states to mostly die out. As local industries declined, breeding programs were closed. California-bred plum cultivars were tried around the world, but with the exception of a few places like Chile and some parts of Italy, they have not thrived as well as they did in California. As a result they were crossed with the local plums of the particular area. In the northern U.S.A., cold-hardy species such as *P. americana, P. nigra* and *P. besseyi* were crossed to the most adapted Japanese types to improve the plums that could be grown there. In the southeastern U.S., the Japanese plums were crossed with the local *P. angustifolia* to enhance disease resistance, resulting in plums such as ‘Bruce’ and ‘Six Weeks’. Unfortunately for modern breeders, only a few of the improved native American selections are still available, since their cultivation is obsolete.

While *P. cerasifera* is a progenitor of European plums, it is a diploid species that is cross-fertile with Asian and American diploid species. These ‘cherry plums’ have not been used much in modern breeding, although two cultivars were selected from chance hybrids with *P. cerasifera*, ‘Methley’ in South Africa and ‘Wilson’ in Australia. *Prunus cerasifera* is a source of earliness, cold-hardiness and probably self-fertility, but fruit size is small.

11.4 Current Breeding Efforts

European plum breeding is naturally concentrated in Europe. Similar goals are important in former Yugoslavia, Romania, Czech Republic, and Bulgaria. Since much of the plum production is dried or processed into brandy and other products, high soluble solids are essential. Releases include both prunes and improved fresh market types. There are at least 10 breeding programs in the former U.S.S.R. They require cold hardiness, modest tree size, self fertility, and productivity. In the more southern zones, larger size (>1 oz, 30 g), higher sugar content (>13%), purple fruit, and earliness are desired. Breeding efforts in Western Europe have increased in recent years. At INRA in Bordeaux, France, goals have been to develop a series of drying prunes and dessert plums that are adapted to French conditions. Cross fertile prunes are needed that produce fruit with similar traits to improve cross pollination and maximize fruit set. Fresh plums are required that ripen before and after ‘Reine Claude’, with equal or better flavor and firmness, and high productivity. In the last 20 years programs have started or restarted in Germany, Switzerland, Sweden and Norway. Most of these efforts are aimed at developing better fresh market plums, with emphasis on disease resistance, particularly plum pox. ‘Stanley’ has been a good parent to transmit tolerance to this disease. In Italy, breeding began at Florence in 1970 to develop early ripening dessert plums with large, high quality fruit and vigorous productive trees. ‘Ruth Gerstetter’ has been the most important parent (Okie and Ramming 1999).

Objectives at Vineland, Ontario are to develop high quality dessert plums to complete a sequence of ripening dates from July to October. Selection criteria are cold hardiness, productivity and blue color. Despite the predominance of the Californian industry in prune production, little intentional breeding has been done there until recently. The University of California at Davis has reinstated their plum breeding project to develop prunes ripening before and after ‘Improved French’. New cultivars must resemble and perform like ‘Improved French’ in order to fit standard production practices for dried fruit. Self pollinated seedlings of ‘French Prune’ display uniformly poor fruit quality, thus it is being crossed with other parents. Over the years other minor breeding programs have existed, the most important of which was USDA breeding at Prosser and later Beltsville, resulting in the recent release of ‘Bluebyrd’. Currently work at USDA-Kearneysville, W.Va. centers on developing bio-engineered plums highly resistant to plum pox virus.

Japanese plum breeding in California has historically focused on size and firmness for shipping. Black skin color became very popular with the introduction of 'Friar' because it did not show bruises and was very productive. However, large, firm, highly colored fruit can be harvested prematurely resulting in reduced consumer quality. Plums showing some ground color may be easier to pick at the proper stage of maturity. Low prices and over-production of black plums have increased interest in other colors. Current objectives include a wider range of skin color and better eating quality. Red or black skin color and yellow or red flesh color appear to be most acceptable although green-skinned plums are shipped to Asian markets. Storage ability, particularly at the end of the season, is also important.

Japanese plum breeding by the USDA at Fresno, California resulted in the releases of 'Frontier' (1967); 'Friar' (1968), the predominant plum in the industry; 'Queen Rosa' (1972); 'Blackamber' (1980), another widely grown plum; and 'Fortune' (1990). 'Fortune', a red plum, represents a shift away from the dark-skinned plums which now predominate in the shipping market. New releases include 'Owen T' and 'John W', a high-quality plum ripe in September notable for its self-fertility (Okie and Ramming 1999).

Private breeders and growers in California have selected many important commercial Japanese plums. Many of the cultivars grown in California were found as chance or open-pollinated seedlings or as mutations, rather than planned hybridizations. Fred Anderson released 'Red Beaut', 'Black Beaut', and 'Grand Rosa'. John Garabedian developed 'Angeleno', still the major late plum. Floyd Zaiger released 'Joanna Red', 'Betty Anne', 'Hiromi Red', and 'Autumn Beaut', as well as 'Citation' rootstock, an interspecific hybrid, and numerous 'plum-apricot hybrids' under the trademarked terms 'pluot' and 'aprium' (some controversy exists over how much apricot blood some of these have in them). Breeders at Sunworld International (formerly Superior Farms) developed 'Black Diamond', 'Black Flame', 'Black Gold', 'Black Torch' and 'Sweet Rosa'. Their program is the largest of the private breeders, and as with most private programs, the releases are patented.

Japanese plum breeding in Europe is relatively new, but will become increasingly important, as demand grows for the large-fruited Japanese plums. Breeders at Rome and Forli are seeking smaller trees to reduce production costs in combination with large size, dark skin, and good eating quality. At Florence, goals are to develop self-fertile, late-blooming plums with high quality, particularly yellow-skinned types. Recently a breeding program has been established near Avignon for southern France where poor weather during pollination is a major problem and Sharka resistance is important. Brazil has three Japanese plum breeding programs aimed at developing lower chill red-fleshed plums with resistance to leaf scald and bacterial spot. Other programs in the Southern Hemisphere are found in South Africa and Australia. Their goals are development of large-fruited, high quality plums with resistance to bacterial spot and bacterial canker, and the ability to store without internal breakdown. Storage ability of four weeks is crucial to exporting the fruit by ship (Okie and Ramming 1999).

The main southern U.S.A. Japanese plum breeding program is USDA-ARS at Byron, Georgia. Their current breeding objectives include those of California plus additional disease resistance. Fruit firmness is somewhat less important because many local markets are available. Resistance is required to three primary diseases: bacterial leaf, fruit spot and twig canker [*Xanthomonas campestris* pv. *pruni* (Smith) Dye], bacterial canker (*Pseudomonas syringae* pv. *syringa*e van Hall), and plum leaf scald (*Xylella fastidiosa* Wells et al.). The first two diseases are problems in many other countries that are trying to grow Japanese plums, such as Australia, New Zealand, Italy, and South Africa. Leaf scald is also a serious problem in Argentina and Brazil. In general, later bloom is more desirable but regions such as Florida and parts of Texas, Australia, and Brazil require even lower chilling requirements than those common in Japanese plums.

11.5 Genetics of Economically Important Traits

Plums genetics have been little studied relative to other crops, because of fewer breeding programs, and the self-incompatibility which makes selfed populations difficult to obtain. However, significant progress has been made in identifying horticulturally useful germplasm.

11.5.1 Pest and Disease Resistance

Plum production is limited by a number of fungal species (Okie and Weinberger 1996, Ramming and Cociu 1991). Brown rot [*Monilinia laxa* (Aderh. & Ruhl.) Honey] is the primary fruit disease in plums and is most important when it is rainy during bloom and fruit-ripening. Cankers caused by several pathogens can affect the longevity of plum trees, particularly in the southeastern United States where black knot [*Apisporina morbosa* (Schw.) ARK.] is a major problem. Leaf blotch (*Polystigma rubrum* Pers.) is an important problem in Europe, while rust [*Tranzschelia discolor* (Fckl.) Tranz. & Litv.] causes significant damage in warm production regions. Other fungal pathogens that are important worldwide include Phytophthora root rot, Armillaria root rot [*Armillaria mellea* (Vahl.:Fr.) P. Kumm], Verticillium wilt (*Verticillium dahliae* Kleb), Powdery mildew [*Podosphaera oxycanthae* (DC.) de Bary], rose mildew [*Sphaerotheca pannosa* (Wallr.:Fr.) Lev.], silver leaf or heart rot [*Stereum purpureum* (Pers.:Fr.) Fr.], plum pockets or bladder plum (*Taphrina communis* and *T. pruni* Tul) and peach scab [*Fusicladium carpophilum* (Thuem.) Oudem]. Shot hole is another common foliar problem that usually is caused by a fungus, *Stigmina carpophila* (Lev.) Ellis, but which can also be a manifestation of a genetic defect that can be overcome by breeding and selection (Weinberger and Thompson 1962).

Resistant genotypes have been identified for Armillaria root rot, black knot, Phytophthora root rot, silver leaf (Ramming and Cociu 1991), fruit spot, twig canker (Okie and Weinberger 1996), leaf blotch, leaf rust (Paunovic 1988) and stem cankers (Norton and Boyhan 1991). Resistance to stem cankers was associated with the spreading growth tree characteristic (Popenoe 1959). Tolerance has been described for plum leaf scald, and powdery mildew (Ramming and Cociu 1991). No source of resistance has been published for plum pockets (Atkinson 1971), bladder plum, peach scab, rose mildew and Verticillium wilt.

Two bacterial diseases are widespread on plums, bacterial canker (*Pseudomonas syringae* pv. *syringae* van Hall) and bacterial leaf spot [*Xanthomonas campestris* pv. *pruni* (Erw. Smith) Dow.]. In the southeastern U.S.A., susceptible cultivars often die before fruiting due to defoliation and dieback. Crown gall [*Agrobacterium tumefaciens* (Smith and Townsend)] is also widespread. Plum leaf scald (*Xylella fastidiosa* Wells) is an important problem in the southeastern U.S.A. Resistant or tolerant genotypes have been identified for all these diseases (Norton et al. 1991, Okie et al. 1992, Okie and Weinberger 1996).

Several viruses have significant negative impacts on plum productivity. Probably the most important is sharka (plum pox), which is found all across Europe and is transmitted by the aphid *Anurophis helicrissi.* Prune brown line, caused by tomato ring spot virus, is an important problem in North America, particularly on 'Stanley'. Other important viruses are Peach mosaic, Prunus ringspot and Rosette. High levels of tolerance are available for all these viruses, but complete resistance has only been described to the tomato ringspot virus (Albrechtova et al. 1989, Hartmann 1994, Ramming and Cociu 1991). A QTL for resistance to sharka has been identified (Dirlewanger et al. 2004a).

Among the most important insect pests on plums are plum curculio (*Conotrachelus nenuphar* Herbst), scale (*Aspidiotus perniciosus* Comstock), mites [*Panonychus silmi* (Koch)] and [*Tetranychus pacificus* (McGregor)], borers [*Synanthedon pictipes* (Grote & Robinson), *Sanninoidea exitiosa* (Say), *Scolytus rugulosus* (Ratzeburg) and *Anarsia lineatella*], fruit flys [*Ceratitis capitata* (Wiedemann), *Dacus dorsalis* Hendel, *Anastrepha ludens* (Loew)], aphids [*Myzus persicae* (Sultzer)] and thrips (Order *Thysanoptera*). There are no published reports of tolerance or resistance to these pests.

Root-knot, lesion and ring nematodes are also major problems wherever *Prunus* are grown. Resistance/tolerance has been reported in rootstocks to all these nematode pests (Okie 1987, Ramming and Cociu 1991). A gene for resistance to the root-knot nematode, *Ma*, has been mapped (Claverie et al. 2004, Dirlewanger et al. 2004b).

11.5.2 Morphological and Physiological Traits

The narrow genetic base of European plum cultivars has limited production to specific areas and made them highly susceptible to the vagaries of nature (Ramming and Cociu 1991). The European plums are restricted to areas with high numbers of chilling hours, cool summers and moderate winters. Many cultivars are self-unfruitful and as a result have poor fruit set during cool, wet pollination seasons. Rain-induced fruit cracking can also be a significant problem, along with shatter pits in some cultivars such as 'Stanley'. Japanese plums have a more diverse background than European ones, although inbreeding has restricted the genetic variability of the most widely grown cultivars (Ramming and Cociu 1991). Some of the key abiotic problems confronting Japanese plum production are susceptibility to spring frosts, insufficient winter hardiness and limited soil adaptations.

Considerable variability has been observed in the chilling requirement, cold hardiness, season of flowering and harvest date of European and Japanese plums, suggesting quantitative inheritance (Table 11.2). Other characteristics that are important in plum breeding are biennial bearing, branching habit and self-fruitfullness. The ability to set buds under high fruit load has been shown to be highly heritable and the spreading habit in *P. domestica* is dominant.

Most of the plum cultivars grown in the world are propagated on rootstocks that are selected for local soil characteristics and vigor requirements. A broad array of

Table 11.2 Genetics of adaptation, productivity, plant habit and fruit quality in plums

Attribute	Observations and sources
Adaptation	
Chilling requirement	Considerable variability exists suggesting quantitative inheritance; low and high chill cultivars have been identified (Okie and Weinberger 1995, Wilson et al. 1975)
Cold hardiness	Considerable variability exists suggesting quantitative inheritance; cold hardy genotypes have been identified (Okie and Weinberger 1995)
Season of flowering	Early and late blooming types have been identified (Okie and Weinberger 1995)
Harvest date	Quantitatively inherited in *P. salicinia* and *P. domestica* (Hansche et al. 1975, Vitanov 1972)
Productivity and habit	
Biennial bearing	Ability to set buds under high fruit load is heritable (Couranjou 1989)
Incompatibility	Most cultivars are self-incompatible, but compatible ones exist; many hybrid plums are poor pollen producers (Okie and Weinberger 1995); S-RNases were identified in plum that shared 84–94% nucleotide identity with other *Prunus* S-RNases (Sutherland et al. 2004)
Spreading habit	Spreading habit in *P. domestica* is dominant (Olden 1965)
Stamen length	Short stamens are dominant in *P. domestica* (Olden 1965)
Fruit quality	
Bloom	Thick bloom on fruit is dominant over thin in *P. domestica* (Okie and Weinberger 1995)
Firmness	Genotypes of *P. salicina* with exceptional firmness have been identified (Yamaguchi and Kyotani 1986)
Flavor	High flavored cultivars have been identified (Okie and Weinberger 1995)
Freestone character	Recessive gene in *P. salicinia* and *P. domestica*; interacts with fruit maturity and firmness (Okie and Weinberger 1995)
Skin color	Generally quantitatively inherited in *P. salicina* and *P. domestica,* although yellow skin is a single recessive gene (Hurter 1962, Weinberger and Thompson 1962, Vitanov 1972)
Shape	Quantitatively inherited in *P. salicina* (Weinberger and Thompson 1962); single locus in *P. domestica* with oval > round > oblong (Okie and Weinberger 1995)
Size/weight	Quantitatively inherited in *P. salicina* and *P. domestica* (Hansche et al. 1975, Weinberger and Thompson 1962)
Sugar content	Quantitatively inherited in *P. domestica* (Hansche et al. 1975)

rootstocks are now available to deal with waterlogging, alkalinity and hardiness (Okie 1987, Ramming and Cociu 1991). The most common rootstocks for European plums include 'Myro 29C', 'Marianna 2624', 'Marianna GF8-1', 'Brompton', 'Damas' and 'St. Julien'. In some areas Japanese plums are also grown on the adapted peach rootstocks, such as 'Lovell', 'Nemaguard' or 'Guardian®'. In other cases, Japanese plums are grown on myrobalan or marianna clonal or seedling stocks.

In cold regions, lack of winter bud hardiness often limits production. *Prunus* from northern climates carry the highest levels of cold-hardiness (Quamme et al. 1982). *Prunus americana* and *P. besseyi* native to the northern states, *P. nigra* native to Canada, and *P. ussuriensis* from northern China carry factors for winter hardiness. In recent years these species have been used more extensively in the former U.S.S.R. to develop hardy plums than in their home countries.

11.5.3 Flower Characters

Bloom time is determined by temperatures throughout the winter and spring. Most European plums require relatively high numbers of chilling hours (probably >1000 hours), whereas most Japanese plums need much fewer ($\sim$ 500–800 hours), meaning Japanese plums usually bloom before European types. The chilling requirements of plums have been little studied, but they seem to respond similarly to peaches. Yields can be reduced in warm regions if chilling hours are insufficient to break the rest period of both flower and leaf buds.

Very low-chill Japanese plums have been developed in Florida, California and Taiwan. Plum cultivars requiring <450 chill hours (below 7°C) include 'Gema de Ouro', 'Golden Talisma', 'Kelsey Paulista', 'Roxa de Itaquera', 'Sanguinea', 'Amerelinha', 'Carmesim' and 'Pluma-7' from Brazil; 'Salad', 'Donsworth', and 'Narrabeen' from Australia, and seedlings from Taiwan (Okie and Weinberger 1996). Other low-chilling plums are 'Reubennel' and 'Harry Pickstone' from South Africa; 'Gulfblaze', 'Gulfbeauty' and 'Gulfrose' from the United States; and 'Remolacha de Capuseo', 'Estrela Purpura', and 'Gigaglia' from Argentina.

Late blossoming can result in greater productivity in an area subject to spring frosts. Breeders in England have attempted to select for high heat requirement to prolong dormancy and delay bloom (Wilson et al. 1975). Northern U.S.A. plum species *P. besseyi* and *P. maritima* bloom very late in Byron, Georgia but fruit well, suggesting they have a higher heat requirement, higher heat threshold, or both, relative to other plums. *Prunus besseyi* has been shown to have a higher heat accumulation threshold than peach (Werner et al. 1988).

Most plum cultivars are self-incompitable and many are poor pollen producers, but highly self fertile ones have been identified (Okie and Weinberger 1996). The S-RNases that regulate self incompatibility in plums have been cloned and sequenced and have been shown to share 84–94% homology with other *Prunus* S-RNases (Sutherland et al. 2004). Since many plum cultivars are self-unfruitful, compatibility with other cultivars can strongly influence productivity. Olden (1965) found short stamens to be dominant in *P. domestica*. Low productivity has reduced the popularity of cultivars derived from native American species in Minnesota (Andersen and Weir 1967). Patterns of compatibility between cultivars are unpredictable, although they have been widely studied (Alderman and Weir 1951, Flory 1947, Tehrani 1991). The general trend is towards self-incompatibility, but compatibility within a ploidy level does occur. Some diploids such as ‘Beauty’, ‘Climax’, ‘Methley’, ‘Friar’, ‘Simka’, and ‘Santa Rosa’ are relatively self-fruitful. Many of the hybrid plums produce little viable pollen, which limits their ability to pollinate regardless of compatibility.

11.5.4 Tree Characters

Tree productivity, essential for successful cultivars, is associated with tree vigor, disease resistance, hardiness and other characteristics. A spreading type tree is easier to manage in the conventional orchard than an upright growing tree. Popenoe (1959) noted that resistance to *Xanthomonas* stem cankers in *P. salicina* cultivars was associated with the spreading growth tree character, perhaps because *P. simonii* as a parent imparted both upright habit and disease susceptibility. Many of the California cultivars have upright growth and bear primarily on spurs. This tree form is preferred for high-density plantings. In the Southeast, vigorous growth can compensate to some extent for the effects of plum leaf scald. Some cultivars such as ‘Harry Pickstone’ and ‘Byrongold’ also bear well on year-old shoots. However, healthy trees of cultivars such as ‘Robusto’ and ‘Segundo’ may be too vigorous, and require both winter and summer pruning to keep the tree open. Many wild plums and some Japanese seedlings, especially juvenile trees, have sharp spurs or thorns, which are unacceptable on commercial plums because they injure both the fruit and the picker, and can even puncture tractor tires.

Crane and Lawrence (1956) reported that purple color of leaves and fruit in *P. cerasifera pissardi* Bailey was controlled by a single pair of genes with heterozygous individuals having intermediate color intensity (as in peach). In *P. domestica* spreading character of growth appears to be recessive. Hairiness of growth and leaves was dominant to sub-glabrous (Olden 1965).

11.5.5 Fruit Quality

A number of factors are key in consumer acceptance of European plums including attractive fruit appearance, large size, firmness, good flavor and texture (Okie and Weinberger 1996). Processing quality is also increasing in importance for drying and brandy making. In the Asian plums, the most important factors are dark skin color and firmness. Several factors associated with plum appearance have been shown to be highly heritable including degree of bloom, color, shape and size (Table 11.2). Thick bloom has been shown to be dominant over thin in *P. domestica*. Skin color is largely quantitatively inherited in *P. domestica*, although yellow skin is regulated by a single recessive gene. Shape has been shown to be quantitatively inherited in *P. salicinia*, while a single locus regulates shape in *P. domestica*.

The fruit quality traits firmness and flavor are also highly heritable and genotypes have been identified that are exceptional for these (Table 11.2). Sugar content has been shown to be quantitatively inherited in *P. domestica* (Hansche et al. 1975). The freestone character in *P. domestica* has been found to be under the regulation of a single, recessive allele, although there is a strong interaction with fruit maturity and firmness. Oval fruit shape was reported to be dominant over round fruit shape which was dominant to oblong; yellow or green skin color recessive to red, purple, blue and black; thick bloom on fruit dominant over thin bloom; and freestone recessive to cling (Okie and Weinberger 1996, Renaud 1975). Hansche et al. (1975) reported fruit size, ripening date, and soluble solids to be highly heritable, in contrast to yield. Vitanov (1972) reported polygenic inheritance for skin color, stone freeness, and ripening date. Genetic factors also affect ability to set buds under heavy crop loads thus avoiding biennial bearing (Couranjou 1989).

The mode of transmission of a few *P. salicina* plum characters has been determined by Weinberger and Thompson (1962). Time of ripening is quantitatively inherited. The average ripening dates of progeny was close to the mid-parent value with some individuals ripening earlier or later than either parent. Size of fruit is also quantitatively inherited. When both parents had large-sized fruit approaching the extreme size, the progeny fruit average smaller in size than that of the parents. Shape of fruit is controlled by multiple factors with neither round nor ovate shape dominant. Yellow skin color is a single gene recessive to red, black, or purple, which intergrade and appear to be quantitatively inherited. Red flesh color is dominant over yellow, and a single factor is involved. The intensity of the anthocyanin color is controlled by multiple genes. Hurter (1962) also found red flesh color dominant over yellow, with monofactorial inheritance. The freestone character is apparently recessive, as occasional seedlings with freestone fruits were found in progeny from clingstone parents. The maturity of the fruit and the firmness of the flesh affects the degree of clinginess. Some plums are ‘air-free’, such that an air pocket surrounds the pit inside the flesh.

Several plum species have fruiting characteristics that would be valuable in a breeding program. *Prunus salicina* hybrids have good size, color, and attractiveness. Some have exceptional firmness and keeping quality. *Prunus cerasifera* plums transmit earliness. They produce progeny which are quite variable in hardiness, fruit form, and other characters even when selfed (Murawski 1959). Tough skin is often carried by *P. americana* which can be used to improve shipping quality.

11.6 Crossing and Evaluation Techniques

11.6.1 Breeding Systems

The European plums (*P. domestica*) are hexaploid ($2n = 48$, $x = 8$). *Prunus spinosa* plums are tetraploids ($2n = 32$). The Japanese plums (*P. salicina*) are diploid ($2n = 16$) as are *P. cerasifera*, *P. americana* and most other species. Since the two leading groups of commercial plums have different chromosome numbers, hybridization between them often gives poor results. Where both parents have the same number of chromosomes, interspecific hybridization is generally successful. Many hybrids have been made, particularly with *P. cerasifera*, *P. salicina*, *P. simonii*, *P. besseyi*, *P. americana*, *P. angustifolia*, *P. hortulana*, *P. munsoniana*, and *P. nigra*. Hybrids have also been made with *P. japonica*, Chinese bush cherry. Hybrids between the first four species and apricot (*P. armeniaca* and *P. mume*) have also been successful, but many are not very productive.

Several plumcots have been introduced ('Red Velvet', 'Royal Velvet', 'Flavor Supreme', 'Flavor Delight', 'Flavor Queen', 'Rutland', 'Plum Parfait', 'Dapple Dandy', 'Spring Satin', 'Yuksa', *P.* × *blireiana*). Others have been grown for generations in southwest Asia as *P.* × *dasycarpa* ('Irani Olju' and 'Tlor Csiran'). Fruit set has been a problem with plumcots, but has improved with some of the newer releases. After backcrossing and intercrossing these plumcots, it becomes difficult to distinguish hybrids from plums. The California industry has recently begun using the term 'interspecific' to describe these plumcot derivatives although the term overlooks the fact that most Japanese plums are already just that. Confusion over what is legally a plum affects marketing orders, grade standards, monetary box assessments, and pesticide usage (Okie and Ramming 1999).

11.6.2 Pollination and Seedling Culture

During the summer, reproductive buds develop in leaf axils. Buds contain either a vegetative axis, or a flower primordia. Initially all reproductive parts are enclosed in the five petals. The five sepals are fused to form a cup at the base of the 5 petals. Plum flowers range in diameter from 5–30 mm, with most commercial plums about 2–3 cm across, with petals opening flat atop the cup-shaped corolla. The 20–30 anthers are attached along with petals to the rim of the calyx cup. The single pistil protrudes above the corolla, but the stigma is positioned only slightly beyond the anthers at full bloom. Some plums form many spurs which carry flower buds, others flower mainly on previous seasons extension growth. For European plums there are usually 1–2 flowers per flower bud, whereas Japanese plum has 3 or more. Some species have as many as 5–6 flowers per bud.

European plums are often self-fertile in contrast to Japanese plums, which usually require ample bees to cross-pollinate the flowers. In practice bees are helpful to increase fruit set in European plums as well, since the often pistil extends above the stamens, and the pollen is little moved by the wind. Since most Japanese plums are self-incompatible, different cultivars blooming at the same time in close proximity are necessary for good fruit set. In years when spring weather inhibits bee flight, fruit set is often inadequate.

For hand pollination by breeders, pollen may be collected by gathering unopened blossoms just before the petals separate. They are placed in a wire screen sieve. Maceration of the flowers forces the anthers through the screen to be collected underneath. Alternately the blossoms can be clipped just above the top of the sepals so that petals and anthers fall into the screen. With gentle tapping the anthers fall through. Pollen produced this way will be cleaner. The anthers are dried overnight at room temperature or with slight extra heating. Pollen is easily shed from the dried anthers by manipulation with a camel's hair brush. Pollen of *P. domestica* can be stored for 550 days at 2°C and 25% humidity, and still produce high percentages of germination. Short-term storage in liquid nitrogen has also been successful. Emasculation of the larger flowers may be performed by grasping the calyx cup with the fingernails and tearing away the unopened corolla. The stamens are attached to the rim and are removed with it. The bare pistil and part of the calyx cup remain. Many breeders have found that fruit set is low after emasculation, perhaps because the pistil is damaged either during emasculation or by weather conditions after pollination. Cultivars of plums which are self-unfruitful do not need to be emasculated before pollination. Using them as seed parents reduces the work of making crosses and improves the chances of obtaining a good set of fruit. Some 'self-unfruitful' cultivars will set a small percentage of blossoms with their own pollen. For breeding purposes this is negligible, but for cytological and genetic studies emasculation is necessary. Cheesecloth, screens or row covers can also be used to enclose a honeybee hive with the tree without using a framework. If the tree is self-fertile, selfed seed can be obtained. Alternately, blooming potted trees or bouquets in buckets of water can be placed inside the cage to provide pollen for the bees to transfer (Okie and Weinberger 1996).

In situations where genetic purity is not essential, breeders often collect open-pollinated seed, particularly from commercial blocks where two desirable parents are interplanted. Some breeders have established small isolated blocks of elite lines. Open-pollinated polycross seed from these trees can be collected in a type of recurrent selection. This approach is particularly useful in producing large progenies where poor adaptation due to climate or disease susceptibility will eliminate many seedlings. Genes for improved adaptability will be concentrated using this approach with less effort expended making hand pollinations. Since many plums are self-infertile, bees can be used to make interspecific pollinations. Species of interest can be planted in the midst of a block of the second species and allowed to open-pollinate. Alternately, caged trees can be used with a beehive and bouquets. Bees are able to effect many more pollinations with less damage than humans.

Seed of early ripening cultivars usually germinate poorly. It is advisable to culture these seed on sterile nutrient agar after removing the endocarp and integuments. Current technology allows the successful culture of ovules as small as 0.6 mm. After-ripening of freshly cultured seed is not necessary, but may be of some help.

Seed of midseason and later-ripening cultivars usually give satisfactory germination when prevented from drying out. The rehydration of dry, stored seed often introduces bacterial and fungal infections.

11.6.3 Evaluation Techniques

Plum breeding work is best accomplished in the regions where the plums will be grown. Each region has its own climatic distinctions in which a new cultivar must be tested to prove its adaptability. High summer temperatures in the San Joaquin Valley of California, for example, can cause internal browning of flesh of some *P. domestica* cultivars. Testing of potential cultivars is more or less a local problem. The 12 most important fruit characters of interest to breeders are: time of maturity, size, shape, crop load, skin color, attractiveness of ground color, color of flesh, firmness, freeness of pit, texture, quality, and resistance to disease. These are not listed in order of importance but rather in sequence in which observations are usually made. Attractiveness is perhaps the most important feature, for a fruit must have consumer appeal to be successful in the markets. It must also be firm enough to arrive in markets in good condition, and must have adequate quality to assure repeat sales.

Plums are generally evaluated in the field when they first fruit 3–5 years after planting. Most breeders only take detailed evaluation notes on seedling trees that meet minimum requirements for vigor and disease resistance, and fruit size. A preliminary field rating for fruit characters identifies trees worthy of follow-up for post-harvest tests. After several years of cropping, seedlings will be propagated by budding and tested in a semi-commercial setting, followed by replicated or commercial trials.

11.7 Biotechnological Approaches to Genetic Improvement

11.7.1 Genetic Mapping and QTL Analysis

Genetic diversity among European *Prunus* rootstocks was assessed using RAPD markers. There was more diversity among *P. domestica* clones than *P. cerasifera* (myrobalan) stocks (Casas et al. 1999). Hexaploid and diploid plum cultivars were also studied, and found to be distinguishable via RAPD markers (Ortiz et al. 1997).

A microsatellite genetic linkage map of myrobalan plum clone P. 2175 and an almond-peach hybrid have been generated (Dirlewanger et al. 2004a,b). The linkage map of plum is composed of 93 markers that cover 524.8 cM. SSR markers from almond-peach as well as apricot were found to be widely transportable across various Prunus species, including plum (Messina et al. 2004). The resistance gene *Ma* was located on linkage group 7. Claverie et al. (2004) was able to use two closely flanking markers to identify a single BAC clone encompassing *Ma*.

11.7.2 Regeneration and Transformation

Adventitious shoots have been regenerated from European plum (*P. domestica*) using cotyledons (Mante et al. 1989), hypocotyls (Mante et al. 1991) and leaves (Novak and Miczynski 1996). Hypocotyl sections were used to produce a transgenic European plum clone, C5, which carried the plum pox virus coat protein gene (PPV-CP) and had strong resistance to all four major serotypes of PPV (Scorza et al. 1994, Ravelonandro et al. 1997). After 5–6 years of natural aphid vectored inoculation, trees of clone C5 remained virus free (Scorza et al. 2003). Other transgenic plum plants carrying the papaya ringspot virus coat protein gene (PRV-CP), delayed symptoms to PPV but the plants eventually became diseased (Scorza et al. 1995).

The expression patterns of the PPV-CP gene has been well studied and hybrids with C5 have been shown to carry the gene and have resistance (Ravelonandro et al. 1998, 2002, Scorza et al. 1998). The resistance of the C5 plants appeared to be RNA-mediated through post-transcriptional gene silencing (PTGS), where transgene mRNA is degraded in the cytoplasm soon after synthesis (Scorza et al. 2001).

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