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Series on Harmonization of Regulatory Oversight in Biotechnology, No. 24

CONSENSUS DOCUMENT ON THE BIOLOGY OF PRUNUS SP. (STONE FRUITS)

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OECD Environment, Health and Safety Publications

Series on Harmonization of Regulatory Oversight in Biotechnology

No. 24

Consensus Document on the Biology of Prunus sp. (Stone fruits)

Environment Directorate

Organisation for Economic Co-operation and Development

Paris 2002

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FOREWORD

The OECD's Working¹ Group on Harmonization of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on the development of *consensus documents* which are mutually acceptable among Member countries. These consensus documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, consensus documents are being published on the biology of certain plant species, on selected traits that may be introduced into plant species, and on biosafety issues arising from certain general types of modifications made to plants.

This document addresses the biology of *Prunus* sp. (Stone fruits). It contains general information about the species, as well as more specific information on taxonomy, crossability, geographic origins, reproductive biology and domestication. It is intended for use by regulatory authorities and others who have responsibility for assessments of transgenic plants proposed for commercialisation, and by those who are actively involved with genetic improvement and intensive management of the genus.

Austria served as lead country in the preparation of this document. It has been revised on a number of occasions based on the input from other member countries. The Joint Meeting of the Chemicals Committee and the Working Party on Chemicals, Pesticides and Biotechnology subsequently recommended that this document be made available to the public.

¹ In August 1998, following a decision by OECD Council to rationalise the names of Committees and Working Groups across the OECD, the name of the "Expert Group on Harmonization of Regulatory Oversight in Biotechnology" became the "Working Group on Harmonization of Regulatory Oversight in Biotechnology."

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Preamble

OECD member countries are now commercialising and marketing agricultural and industrial products of modern biotechnology. They have identified the need for harmonization of regulatory approaches for the assessment of these products, in order to avoid unnecessary trade barriers.

In 1993, **Commercialisation of Agricultural Products Derived through Modern Biotechnology** was instituted as a joint project of the OECD's Environment Policy Committee and its Committee on Agriculture. The objective of this project is to assist countries in their regulatory oversight of agricultural products derived through modern biotechnology – specifically in their efforts to ensure safety, to make oversight policies more transparent and efficient, and to facilitate trade. The project is focused on the review of national policies, with respect to regulatory oversight, that will affect the movement of these products into the marketplace.

The first step of this project was to carry out a survey concentrating on national policies in regard to regulatory oversight of these products. Data requirements for products produced through modern biotechnology, and mechanisms for data assessment, were also surveyed. The results were published in *Commercialisation of Agricultural Products Derived through Modern Biotechnology: Survey Results* (OECD, 1995).

Subsequently, an OECD workshop was held in June 1994 in Washington, D.C. with the aim of improving awareness and understanding of the various systems of regulatory oversight developed for agricultural products of biotechnology; identifying similarities and differences in various approaches; and identifying the most appropriate role for the OECD in further work towards harmonization of these approaches. Approximately 80 experts in the areas of environmental biosafety, novel food safety and varietal seed certification, representing 16 OECD countries, eight non-member countries, the European Commission and several international organisations, participated in the workshop. *Report of the OECD Workshop on the Commercialisation of Agricultural Products Derived through Modern Biotechnology* was also published by the OECD in 1995.

As a next step towards harmonization, the Working Group on Harmonization of Regulatory Oversight in Biotechnology instituted the development of **consensus documents** that are **mutually recognised** among member countries. The purpose of these documents is to describe common elements in the safety assessment of a new plant variety developed through modern biotechnology, to encourage information sharing and prevent duplication of effort among countries. These common elements fall into three general categories: the biology of the host plant species, or crop; the introduced genes and gene products conferring the novel trait; and biosafety issues arising from the introduction of certain general trait types into plants.

This consensus document is a “snapshot” of current information that may be relevant in a regulatory risk assessment. It is meant to be useful not only to regulatory officials, as a general guide and reference source, but also to industry and others carrying out research and product development.

It is anticipated that this consensus document and others in the plant biology series, together with the relevant consensus documents on genes and products that confer novel traits in plants as well as those providing information on biosafety issues arising from the use of general trait types in plants, will be of use in the biosafety assessment of genetically modified plants.

Reference to two other OECD publications that have been published in recent years will also prove useful. *Traditional Crop Breeding Practices: An Historical Review to Serve as a Baseline for Assessing the Role of Modern Biotechnology* presents information concerning 17 different crop plants. It includes sections on phytosanitary considerations in the movement of germplasm and on current end uses of the crop plants. There is also a detailed section on current breeding practices. *Safety Considerations for Biotechnology: Scale-Up of Crop Plants* provides a background on plant breeding, discusses scale dependency effects, and identifies various safety issues related to the release of plants with “novel traits”.²

To ensure that scientific and technical developments are taken into account, OECD countries have agreed that consensus documents will be updated regularly. Additional areas relevant to the subject of each consensus document will be considered at the time of updating.

Users are therefore invited to provide relevant new scientific and technical information, and to make proposals concerning additional areas that might be considered in the future. ***A short, pre-addressed questionnaire is included at the end of this document. The information requested should be sent to the OECD at one of the addresses shown.***

2. For more information on these and other OECD publications, contact the OECD Publications Service, 2 rue André-Pascal, 75775 Paris Cedex 16, France. Fax: (33) 01.49.10.42.76; E-mail: Pubsinq@oecd.org; or consult <http://www.oecd.org>

Section I - Introduction

1.1. General Background

The genus of *Prunus sensu lato* comprises more domesticated (also cultivated) species of temperate fruits than the other genera in the family of *Rosaceae* (*Malus*, *Pyrus*, *Sorbus*, *Cydonia*, *Rubus*, *Fragaria*). One of the obvious reasons for the abundant domestication might have been the coincidence between the location of the centre of variability of *Prunus* and the site of human evolution and/or of the first ancient high civilisations of human history.

Improvement of fruit trees through traditional breeding methods is a long-term effort because of their lengthy generation time. Thus, new approaches are researched to attain the envisaged breeding goals in a reasonable time frame. Genetic transformation is potentially useful, because specific genetic changes can be made. In the last few years successful examples of resistance breeding against viruses from different plant virus families have been reported, using the coat protein-mediated cross protection approach (Beachy et al., 1990). However, only very few fruit trees have been among these experiments due to the difficulties in transformation protocols.

“Cross protection” was originally described as the phenomenon of protection of a plant against the invasion of a severe disease-causing virus due to prior inoculation of the plant with an attenuated virus strain (McKinney, 1929). Hamilton postulated in 1980 that the expression of sequences from the viral genome, if expressed in transgenic plants, could possibly cause a protection against viruses. In fact by the expression of the viral coat protein gene in transgenic plants, similar effects could be obtained, and it was therefore distinguished as coat protein mediated protection (Beachy et al., 1990).

This still continues to be a difficult task among fruit trees, as can be seen from the limited number of successful reports of regeneration in woody species (McGranahan et al., 1988; Laimer da Câmara Machado et al., 1989; James and Dandekar, 1991; Oliveira and Pais, 1992; Mante et al., 1991) and in *Prunus* species, in particular plum (Scorza et al., 1994; Ravelonandro et al., 1997) peach (Hammerschlag et al., 1989), apricot and cherry rootstocks (Laimer da Câmara Machado et al., 1992; da Câmara Machado et al., 1995a,b).

1.2. Topics for this case study

One subject of the present study is to assess tools intended to cope with the new plagues, such as the currently incurable Plum Pox Virus (PPV) disease, which harass the growth of *Prunus* species and endanger the mere existence of the most precious, highly esteemed ancient, as well as, new cultivars.

Attempts at developing GMOs have been initiated by several research teams around the world and on such crops as plums (Scorza et al., 1994) and apricots (Laimer da Câmara Machado et al., 1992; da Câmara Machado et al., 1995c). Similar research is currently sponsored in Hungary, especially, to save the traditional plum variety, Besztercei. This precious local variety found fame in the last century in Hungarian

and later Bosnian dried fruit, jam, distilled beverages, etc. The rapid decline of plum production ensued, as surmised, with the release of viruses triggered by the developing trade of nursery grown graftings. The plum growing regions of the former Yugoslavia were hit most severely. As a result, the original site of the variety Besztercei was assigned to Romania after the First World War. Traditional breeding to find or to introduce resistance to PPV started about the middle of the 20th century at Cacak (former Yugoslavia). In parallel, surveys of varieties resistant or at least less affected by PPV were undertaken, but, little hope exists of finding a solution (Cociu et al., 1997; Hartmann, 1988).

In this study, an attempt is also made to provide background information for science-based decision making, in case such GMOs should be released into the environment. As well, this study focusses the assessment on risks and develops strategies for avoiding or counteracting said risks.

Section II - Biology of *Prunus* sp.

2.1. General Description and use as a crop

The genus *Prunus* is comprised of approximately 400 species of trees and shrubs. Many species and cultivars are grown for their edible fruits, while others are planted for their ornamental value. Approximately 25 species are native to the US, of which 18 reach tree size (Maynard et al., 1991). Like *P. avium* L. in Europe, black cherry (*P. serotina* Ehrh.) is the only member of this genus with commercial importance as a timber species in the US (Fowells, 1965). It is a high-value hardwood timber species, prized for cabinetry, furniture and veneer (Panshin and De Zeeuw, 1970).

Stone fruits (Table 1) are appreciated world-wide either for fresh consumption, or in the processing industry: drying, distillation, canning, production of jams, syrups and fruit juices, etc. (Druart and Gruselle, 1986). As well, they are used for their timber and their value as ornamental crops (Moore and Ballington, 1991).

Table 1: Stone fruit production (1000 metric tonnes) in the world from 1989 through 1999

Crop	1989-91	1997	1999
Peaches and nectarines	9317	11286	12044
Plums	6270	7845	7346
Apricots	2226	2375	2720
Almonds	1288	1554	1632

Source: FAO Production Yearbook 1999

Plum species are found native throughout the Northern Hemisphere but mostly in the temperate zone. The earliest writings about plums date back some 2,000 years (Gautier, 1977). Plums may have been the first species among all the fruits to attract human interest. It is more remarkable that the earliest cultivation of *P. domestica* began somewhere between Eastern Europe and the Caucasian mountains, whereas *P. salicina* and *P. simonii* were brought into cultivation in Asia.

It is remarkable that other cultivated temperate fruits of the *Prunus* genus, apricot and peach, reached Europe even before the Roman empire. The Latin names of the crops refer to Armenia and Persia, respectively, indicating the path of trade in ancient times. The centre of origin of those species is rather diffuse, but much more in the East, i.e. in Central and East Asia. Both species “grew up” as important crops in modern Europe. Some of the reasons might be their abundance and associated wealth as well as, a whole year round offer of subtropical fruits competing with the short season temperate fruits.

The peach is one of the most varied of all fruit species, falling between trees and shrubs of fruit. There are several types of them in the canopy, vegetative and generative characteristics, namely fruit, stone and seed traits. All commercial cultivars belong to *P. persica* L. Batsch, and are primarily grown in

temperate zones between latitudes 30° and 45° N and S, and in the tropics and subtropics at higher elevations (Hammerschlag, 1986).

A close relative of the peach, the almond, represents an entirely different food quality. Its cultivation in generally dry, if not marginal habitats, is as extensive as an almost semi-domesticated fruit, less subject to phytosanitary problems. Interspecific hybrids of *P. amygdalus* and *P. persica* are well known in fruit growing as an important rootstock for peach production, e.g., GF 677.

A somewhat detached subgenus of the genus *Prunus* includes the cherry and sour cherry which are, equally, ancient cultivated fruits, one of them being diploid, the other, tetraploid.

P. avium is primarily a European species, which occurs abundantly in wild form on the forest slopes of Southern, Central and Western Europe. Pomologically, according to fruit firmness, cherry cultivars are divided into the Heart cherry group, with mainly early ripening cultivars that have a soft flesh, and the Bigarreau group. The Bigarreau group includes late cultivars with firm flesh, such as Lambert, Stella, Bing, Van, Windsor, Schmidt, Hedelfingen, Napoleon, and Gold that have dark red, black, yellowish or light-coloured fruits. The major portion of the harvest is processed into solid, liquid or frozen products, and part is kept for direct consumption in the fresh state (Ivanicka and Pretová, 1986).

Sour cherry is widely naturalised and its distribution area covers almost all European countries and SW Asia. However, it is cultivated in many other parts of the world, mainly in North America. Sour cherry production is about one-third that of sweet cherry (FAO Yearbook, 1975, data not included in later editions). More recent data (in thousands tons) indicate that the most important producers are the USSR with 450 (Kramer, 1985) and the USA with 119 (Westwood, 1978). Other countries with great productions are: Germany (91), Former Yugoslavia (47), and Hungary (41) (Christensen, 1985; Kramer, 1985). Although the most important cultivars used are Schattenmorelle and Montmorency, the list of cultivars reaches a great number. Thus, in the USSR it runs up to 80 sour cherry varieties listed in various district catalogs (Kramer, 1985). The use of Stockton Morello in North America as a cherry rootstock is very minor (Tukey, 1964). The predominant root stocks in North America are mazzard (*Prunus avium*) or *P. mahaleb*.

The predominance of one or two major apricot cultivars in each production area is partly responsible for large fluctuations in yield and makes this crop species vulnerable to adverse environmental conditions, diseases and pests (Mehlenbacher et al., 1991). Moreover, the major cultivars of the main apricot producing countries (Spain, Italy, the United States, Greece, France, Morocco, Hungary, Romania, South Africa, Bulgaria, Australia, Algeria) belong to the European group, which by their origin are known to have a very narrow genetic background (Kostina, 1969).

Apricot production is rapidly changing in Europe. Spain, the main producer keeps its production constant, while France is increasing production and Italy and Greece are decreasing their production levels.

Especially drastic is the situation in Greece, where the annual production of 100,000 tonnes about 10 years ago has decreased to 30-50,000 tonnes, mainly due to damage caused by late frosts and the Sharka virus.

The same holds true for Hungary, where at the beginning of the Seventies 60-130,000 tons were produced on an area of 13-14,000 ha, while in the early 90s the orchard area decreased to 2,500 – 3,000 ha and production dropped to 20-40,000 tons/a (Pedryc, Budapest, pers. comm).

2.2. Taxonomic Situation

2.2.1. Taxonomy

In the past different approaches were chosen to present the phylogeny of the subfamily of *Prunoideae* belonging to the family of *Rosaceae*. There were two main contrasting conceptions, i.e. all stone fruits belong to the genus *Prunus*, or the genus *Prunus* contains only plums and prunes. Here the classification is presented according to Strasburger et al. (1991).

The seven subgenera in *Prunus* are determined basically by how the leaves are rolled up in the bud, whether the flowers are organised in cymes or in racemes and finally by morphological characteristics of the generative organs, i.e. the size and colour of flowers, fruit, stone and seed traits.

- AMYGDALUS (almonds): *P. amygdalus*, *P. bucharica*, *P. fenzliana*, *P. kuramica*, *P. nana*, *P. orientalis*, *P. webbii*
- PERSICA (peaches): *P. davidiana*, *P. ferganensis*, *P. kansuensis*, *P. mira*, ***P. persica***
- ARMENIACA (apricots): *P. ansu*, ***P. armeniaca***, *P. brigantiaca*, *P. x dasycarpa*, *P. holosericea*, *P. mandshurica*, *P. mume*, *P. sibirica*
- PRUNUS (plums and prunes): *P. cerasifera*, *P. divaricata*, ***P. domestica***, *P. insititia*, *P. italica*, *P. spinosa*, *P. syriaca*, ***P. salicina***, *P. simonii*, *P. ussuriensis*, *P. americana*, *P. angustifolia*, *P. hortulana*, *P. maritima*, *P. mexicana*, *P. munsoniana*, *P. nigra*, *P. rivularis*, *P. subcordata*
- CERASUS (sweet and sour cherries): ***P. avium***, ***P. cerasus***, *P. fruticosa*, *P. japonica*, *P. maackii*, *P. mahaleb*, *P. pseudocerasus*, *P. pumila*, *P. serrulata*, *P. tomentosa*
- PADUS (bird cherries) *P. padus*, *P. serotina*
- LAUROCERASUS (bay-cherries)

This study will focus on essential data about the species in bold (*P. amygdalus*, *P. persica*, *P. armeniaca*, *P. domestica*, *P. avium*, *P. cerasus* and *P. salicina*), since they are the most widely grown species with horticultural interest. However, interactions with wild or escaped relatives will also be considered.

2.2.2. Number of chromosomes

The phenomenon of polyploidy is a widespread occurrence and of great importance in the evolution of new species or forms. For example, many genera of flowering plants contain a series of species characterised by varying degrees of ploidy. Polyploidy is important, too, from a practical point of view, since plants with this character are often very vigorous, and may be more resistant to frost and the attacks of parasitic fungi. Moreover, changes of flower structure and self-fertility according to the number of chromosomes have been observed. In *Prunus*, the basic number in vegetative cells is eight chromosomes. Polyploidy, due to interspecific hybridization, took place during the phylogeny of the genus and is responsible for self-sterility and intersterility. The C-value is the DNA amount in the unreplicated haploid nucleus (pg/cell). The DNA amount in the unreplicated haploid or gametic nucleus of an organism is referred to as its C-value (Swift, 1950), irrespective of the ploidy level of the taxon. C-value equals genome size in diploid species, but always exceeds genome size in polyploid species. Nuclear DNA C-

value and genome size are important biodiversity characters with fundamental biological significance and many uses (Bennett and Leitch, 1995).

The following different number of chromosomes and degrees of ploidy have been reported:

Genus	Species	Chromosome number	Reference
Amygdalus	<i>P. amygdalus</i>	2n=16 (diploid)	Darlington et al., 1945
	<i>P. bucharica</i>	2n=16 (diploid)	
	<i>P. fenzliana</i>	2n=16 (diploid)	Darlington et al., 1945
	<i>P. kuramica</i>	2n=16 (diploid)	
	<i>P. orientalis</i>	2n=16 (diploid)	
	<i>P. tenella</i>	2n=16 (diploid)	Darlington et al., 1945

The cultivated almond was designated *Amygdalus communis* L. by Linnaeus in 1753. Miller (Webb, 1967) first used the name *Prunus* in 1768 in designating the cultivated 'sweet' almond as *Prunus dulcis*, describing it apparently as a 'botanical variety'. The species was later named *Prunus amygdalus* by Batsch (1801), the species name meaning 'Greek nut.' Archangeli (1882) later used the name *Prunus communis* for almond. Schneider (1904) and Rehder (1924) accepted *Prunus amygdalus* Batsch as the scientific name for almond and by which the species had been known in American botanical and horticultural literature for many years. In 1964, a discrepancy in name priority was determined to exist by the General Committee of Botanical Nomenclature of the International Botanical Congress (Punt, 1964). As a result, the name *Prunus dulcis* (Miller) D.A.Webb was proposed for the cultivated sweet almond (Webb, 1967). *Prunus amygdalus* Batsch (1801) and *Prunus communis* L. Archangeli (1882) are listed as synonyms. A flowering almond species appreciated as an ornamental is *Prunus triloba*.

Genus	Species	DNA amount 2C (pg)	Chromosome number	Reference
<i>Persica</i>	<i>P. davidiana</i>		2n=16 (diploid)	Missouri Botanical Garden, 1990
	<i>P. ferganensis</i>		2n=16 (diploid)	Missouri Botanical Garden, 1991
	<i>P. kansuensis</i>		2n=16 (diploid)	Missouri Botanical Garden, 1990
	<i>P. mira</i>		2n=16 (diploid)	
	<i>P. persica</i>	0.6	2n=16 (diploid)	Darlington et al., 1945 Bennett and Leitch, 1995

It has been suggested by Watkins (1979) that almond and peach, which are both regular diploids (2n = 16) originated from the same primitive species but evolved separately following the mountain development of the Central Asian massif. Almonds evolved in the arid steppes, deserts and mountainous areas to the west, south and southwest, whereas the peach evolved eastward towards China in a more humid environment and at lower elevations.

Genus	Species	DNA amount 2C (pg)	Chromosome number	Reference
<i>Armeniaca</i>	<i>P. ansu</i>		2n=16 (diploid)	
	<i>P. armeniaca</i>	0.6	2n=16 (diploid)	Darlington et al., 1945 Bennett and Leitch, 1995
	<i>P. brigantiaca</i>		2n=16 (diploid)	
	<i>P. mandshurica</i>		2n=16 (diploid)	
	<i>P. x dasycarpa</i>		2n=16 (diploid)	
	<i>P. holosericea</i>		2n=16 (diploid)	
	<i>P. mume</i>		2n=16 (diploid), 24	Darlington et al., 1945
	<i>P. sibirica</i>		2n=16 (diploid)	

All apricot species are regular diploids with eight pairs of chromosomes (2n=16). No difficulties have been reported in intercrossing *P. armeniaca*, *P. sibirica*, *P. mandshurica* and *P. mume*, although not all combinations have been attempted.

P. x dasycarpa Ehrh., the black or purple apricot, is a naturally occurring hybrid of *P. cerasifera* Ehrh. and *P. armeniaca* and is found as isolated trees, where the distribution of the two species overlaps (Mehlenbacher et al., 1991). *P. x dasycarpa* has been backcrossed to both *P. cerasifera* and *P. armeniaca*; crosses to the plum parent are generally easier.

Genus	Species	DNA amount 2C (pg)	Chromosome number	Reference
<i>Prunus</i>	<i>P. americana</i>		2n=16 (diploid)	Darlington et al., 1945
	<i>P. angustifolia</i>		2n=16 (diploid)	Janick and Moore, 1975
	<i>P. cerasifera</i>		2n=16 (diploid), 24	Janick and Moore, 1975
	<i>P. domestica</i>	1.8	2n=48 (hexaploid)	Darlington et al., 1945 Bennett and Leitch, 1995
	<i>P. hortulana</i>		2n=16 (diploid)	Janick and Moore, 1975
	<i>P. insititia</i>		2n=48 (hexaploid), 24	Darlington, 1945, Tischler, 1950
	<i>P. italica</i>		2n=48 (hexaploid)	
	<i>P. maritima</i>		2n=16 (diploid)	Darlington et al., 1945
	<i>P. mexicana</i>		2n=16 (diploid)	Janick and Moore, 1975
	<i>P. munsoniana</i>		2n=16 (diploid)	Janick and Moore, 1975
	<i>P. nigra</i>		2n=16 (diploid)	Darlington et al., 1945
	<i>P. rivularis</i>		2n=16 (diploid)	Janick and Moore, 1975
	<i>P. salicina</i>		2n=16 (diploid)	Darlington et al., 1945
	<i>P. simonii</i>		2n=16 (diploid)	Janick and Moore, 1975
	<i>P. spinosa</i>		2n=32(tetraploid), and natural hybrids with 16, 24, 40, 48	Darlington et al., 1945, Janick and Moore, 1975
	<i>P. subcordata</i>		2n=16 (diploid)	Janick and Moore, 1975
	<i>P. salicina</i>		2n=16 (diploid)	Darlington et al., 1945, Janick and Moore, 1975
	<i>P. syriaca</i>		2n=16 (diploid)	
	<i>P. ussuriensis</i>		2n=16 (diploid)	

The most important commercial species of plums are generally classified in two groups, the European plums (*Prunus domestica* L.) and related forms with hexaploid chromosome number (2n=6x=48) and the Japanese plums (*Prunus salicina*) and their hybrids with diploid chromosome number.

P. domestica is believed to have arisen as a natural allopolyploid between *Prunus cerasifera* (diploid) and *P. spinosa* (tetraploid) (Crane and Lawrence, 1952).

Genus	Species	DNA amount 2C (pg)	Chromosome number	Reference
<i>Cerasus</i>	<i>Prunus avium</i>	0.7	2n=16 (diploid), 24, 32	Darlington et al., 1945 Bennett and Leitch, 1995
	<i>P. besseyi</i>		2n=16 (diploid)	
	<i>P. cerasus</i>	1.2	2n=32 (tetraploid)	Missouri Botanical Garden, 1985 Bennett and Leitch, 1995
	<i>P. fruticosa</i>		2n=32 (tetraploid)	
	<i>P. mahaleb</i>		2n=16 (diploid)	Darlington et al., 1945
	<i>P. pumila</i>		2n=16 (diploid)	Darlington et al., 1945
	<i>P. serrulata</i>		2n=16 (diploid), 24	Darlington et al., 1945
	<i>P. subhirtella</i>	0.6	2n=16 (diploid)	Darlington et al., 1945 Bennett and Leitch, 1995
	<i>P. tomentosa</i>		2n=16 (diploid)	Darlington et al., 1945

Among cherries, the sweet (*P. avium*) and sour (*P. cerasus*) cherry, flowering ornamental cherry species, and a few others used as rootstocks for cherries are important. The earliest description of the “keration” comes from Theophrastus about 300 B.C. *P. fruticosa*, the ground cherry, is considered the probable parent of both *P. avium* and *P. cerasus*, sweet and sour cherry respectively (Fogle, 1975).

The chromosome number of *P. cerasus* is 32 (Crane and Lawrence, 1952). As 8 is the base number of the genus *Prunus* and following De Candolle’s hypothesis (Coutanceau 1953) it seems that sour cherry is a tetraploid originating from an unreduced *P. avium* (2n = 16) gametophyte, thus by chromosome doubling.

Genus	Species	DNA amount 2C (pg)	Chromosome number	Reference
<i>Padus</i>	<i>P. padus</i>		2n=16 (diploid)	Tischler, 1950
	<i>P. serotina</i>	1.0	2n=32 (tetraploid)	Kumar and Subramanian, 1987 Bennett and Leitch, 1995

2.2.3. Molecular markers for the identification of genotypes

Since morphological markers sometimes are prone to equivocal interpretations and generally time consuming, the search for biochemical and molecular markers was initiated in the genus *Prunus*. The development of DNA markers like RFLPs or RAPDs is very recent in fruit trees (Eldredge et al., 1992).

Initially, isoenzyme markers in *Prunus* crops like peach (Messeguer et al., 1987; Monet and Gribault, 1991), almond (Cerezo et al., 1989; Arús et al., 1994a) and cherry (Santi and Lemoine, 1990; Boskovic and Tobutt, 1994) were developed.

In addition to the isozyme markers, RAPD, RFLP and AFLP (Arús et al., 1994a,b) which are used to clearly distinguish among the different stone fruit cultivars available on the international fruit market, additional markers, such as SSRs have recently been developed for peach (Cipriani et al., 1999) and apricot (da Camara Machado et. al., submitted).

2.3. Centres of origin/diversity

2.3.1. Geographic origin and natural distribution of *P. amygdalus*

Populations of almond have been described to occur in two areas: (a) the south west slopes and deep gorges of Kopet-Dagh Mountains of Turkmenistan (800-1700m), in an area, which is dry and snowless and (b) in Uzbekistan on the western slopes of the Tian Shan Mountains at similar elevations.

The almond *Prunus dulcis* (Miller) D.A Webb has been grown in cultivation for its edible seed since ancient times. From its centre of origin in Central Asia, it was disseminated to all ancient civilization in Asia (2000 BC), Europe (350 B.C.), and North Africa (600-700 A.D.) (Vavilov, 1930; deCandolle, 1964). Almonds were initially introduced into California during the Spanish Mission Period, but significant plantings were not made until after the settlement of California following the Gold Rush (Wickson, 1910; Wood, 1925; Taylor and Philip, 1925). During the same period (1850-1900), almonds were introduced into West Australia (Quinn, 1928), South Africa, and parts of South America (particularly Chile and Argentina) in regions with the same climate as California.

Almond production is concentrated in three regions of the World: Asia, Mediterranean area (of Europe and Africa) and California (Kester and Horel, 1980).

The different species have different geographic distributions:

- *P. amygdalus* Batsch. syn. *P. communis* Arcang. is native in the south west slopes and deep gorges of the Kopet-Dagh and western slopes of the Tien-Shan Mountains
- *P. bucharica* (Korsh.) Fedtsch. is native in the steppes of Central Asia
- *P. fenzliana* Fritsch. is distributed in the Caucasian Mountains, near Ararat and Armenia
- *P. kuramica* Korchinsky is feral native in slopes of the Hindukush Mountains
- *P. orientalis* Mill. is distributed in South-central Asia
- *P. webbii* (Spach) Vieh., a European almond species, which is found in the Balkans
- *P. tenella* is a European almond species with strong sprouting ability

2.3.2. Geographic origin and natural distribution of *P. persica*

Peaches are native to China and its culture dates back at least 4000 years (Wang, 1985). Wild peaches are known as “Maotao” (hairy peach) or “Yitao” (wild peach) currently exist in remote areas of China, where they are used as seedling rootstock for improved cultivars (Li, 1984). The Chinese recognize three groups of peaches (Li, 1984; Wang, 1985). The Southern group of peach is grown along the Yangtze River in the provinces of Jiangsu, Zhejiang, Jiangxi, Hubei, Hunan and Sichuan. The Northern group of peach is found along the Yellow River in Shandong, Hebei, Henan, Shanxi, Shaanxi, and Gansu provinces, and a third group is found in the arid northwest of China. Peaches spread west from China following the trade routes through Persia. In Egypt, peaches were used in offerings to the “God of Tranquillity” about

1400 B.C. (Roach, 1985). According to Plinius, the peach was planted in Greece by 332 B.C. and was mentioned by Virgil (70-19 B.C.) in Roman literature. Along the path of distribution through Europe, adapted populations of local peaches can be found. Among these are the “vineyard” peaches of France, Romania, and the former Yugoslavia (Parnia et al., 1988) towards the Hungarian Great Plain. The peach was common in England by the 14th century (Bunyard, 1938). Peaches were brought to North and South America by the early Spanish explorers through St. Augustine, Florida and to settlements in Mexico by 1600.

Five species are considered as peaches:

- *P. davidiana* (Carr.) Franch. is native of North China
- *P. ferganensis* (Kost. et Rjyb.) Kov. et Kost., which is found in Western China
- *P. kansuensis* Rehd., which is native in North-western China
- *P. mira* Koehne, which is found in the Himalayan mountains and along the Yellow and Yangtze Rivers
- *P. persica* (L.) Batsch. which contains most of the cultivated peaches and nectarines (convarietas *leavis*), be it freestone (provar. *glabra*) or clingstone (provar. *nudicarpa*).

2.3.3. Geographic origin and natural distribution of *P. armeniaca*

Prunus armeniaca L., the cultivated apricot, is believed to have originated in the mountains of Northern and North-eastern China in the same area as the Great Wall and overlapping the southern branch of the distribution of *P. sibirica* L. (Mehlenbacher et al., 1991). The apricot was brought via Armenia and Asia Minor into Italy over 2000 years ago, to England in the 13th century and to North America only by 1720 (Westwood, 1978).

Wild apricots also occur in the Tien Shan Mountains in the Xinijang autonomous region (Wang, 1985) and Dzhungar and Zailing Mountains in Soviet Central Asia. This is believed to be the secondary centre of origin (Zeven and de Wet, 1982). The area of distribution of the cultivated apricot is much larger and includes areas where seedling orchards are common such as Central Asia, Afghanistan, Kashmir, Iran, Turkey, and Trans-Caucasia (Kostina, 1936; Mehlenbacher et al., 1991). All of these areas are valuable sources of germplasm.

Apricot production is severely restricted by ecological conditions. The gene pool of apricot contains only few species and varieties, which range in areas of adaptation from the cold winters of Siberia to the subtropical climate of North Africa and from California, the deserts of Central Asia and the humid areas of Japan and Eastern China. However, commercial production areas are still very limited (Mehlenbacher et al., 1991; Faust - Surányi and Nyujtó, 1998).

In China, the Yu's order (2200 B.C.) refers to apricot growing and there are also documents from the 7th century (Löschning and Passecker, 1954; Nyujtó and Surányi, 1981; Faust et al., 1998). Kostina (1969) presented an excellent eco-geographical grouping for apricot cultivars and species. There are Central Asian, Irano-Caucasian, European, Northern Chinese, Tibetan, North-eastern Chinese, Eastern Chinese and Dshungar-Zailij groups (Faust et al., 1998; Mehlenbacher et al., 1991). Basic species are identified, as follows:

- *P. ansu* Maxim. is distributed in Eastern China, South Korea and Japan
- *P. armeniaca* L. is native of Northern and North-eastern China
- *P. brigantiaca* Vill. (Alpine apricot) is distributed in the region of the Alps, in South-eastern France
- *P. mandshurica* (Maxim.) Koehne is native in north east of China
- *P. x dasycarpa*, a hybrid between *P. cerasifera* and *P. armeniaca* Ehrh.
- *P. holosericea* (Batal) Kost. (Tibetan apricot), which is native of Tibetan Mountains
- *P. mume* (Sieb.) Sieb. et Zucc., which is native in south of China
- *P. sibirica* L., which is distributed along Baikal Lake, Mandshuria, North Korea

2.3.4. Geographic origin and natural distribution of *P. domestica* and *P. salicina*

Plum species are found native throughout the Northern Hemisphere but mostly in the temperate zone. The earliest writings about plums date back some 2000 years (Cullinan, 1937) and De Candolle assumes that plums have been known for 2000-4000 years (Banegal, 1954).

Prunus domestica seems to have originated in Southern Europe or Western Asia around the Caucasus Mountains and the Caspian sea (Cullinan, 1937). However, it is also widespread in the Balkans and Mediterranean countries.

Prunus salicina originated in China and was introduced into Japan 200-400 years ago. In China, it has been cultivated since ancient times where it is thought to occur in the wild in the Tsunglin range in Shensi and Kansu. Recently, it reached Europe by way of California and Italy.

Plums are a diverse group of plants with many botanical species, that have been cultivated for the last 3000 years. The most important species of *Prunus* are generally classified into three groups, the European, the Asian and the American plums. Plums may have been the first species among all the fruits to attract human interest. Six of the most important species of plums, *P. domestica*, *P. italica*, *P. syriaca*, *P. salicina*, *P. simonii* and *P. americana* are not known in the wild and presumably were selected and cultivated very early by humans. It is more remarkable that the earliest cultivation of *P. domestica* began somewhere between Eastern Europe and the Caucasian mountains, whereas *P. salicina* and *P. simonii* were brought into cultivation in Asia.

Regarding the Krieche/Haferpflaume (*P. insistitia* var. *juliana*), repeatedly described as “wild”, Körber-Grohne (1996) mentions, that this is not the case in SW-Germany. As a welcome fruiting shrub, it has served as a shrubby hedge (Hag) around farm gardens or as a division between fruit orchards. It is not present in hedges or open fields nor is it found in woods or wood margins, as is the case with the crab apple. The oldest subfossil fruitstones have been found in Neolithic settlements in Germany and Switzerland (Ehrenstein, Robenhausen). The Krieche/Haferpflaume (*P. insistitia* var. *juliana*) is a typical example of the continuity of domestication from the Neolithic until the present, which has been attributed to the propagation by grafting from Roman times onwards, or in the case of plum cultivars through root suckers.

The classification of plums is divided into geographic groups:

European group	<i>P. spinosa</i> L.	Europe, Asia Minor and North Africa
	<i>P. cerasifera</i> Ehrh. (and <i>P. divaricata</i> Ledeb.)	With some eco-geographical subspecies in Balkan, Asia Minor, Caucasian region and Central Asia
	<i>P. insititia</i> L.	In Central Europe, Balkan, Western Asia
	<i>P. domestica</i> L.	Native in Western Asia
	<i>P. italica</i> (Borkh.) em. Kárpáti	Hybrid between <i>P. domestica</i> and <i>P. insititia</i> with convarietas (<i>pomariarum</i> , <i>claudiana</i> , <i>ovoidea</i> and <i>mamillaris</i>)
	<i>P. syriaca</i> (Borkh.) em. Kárpáti	Hybrid between <i>P. cerasifera</i> and <i>P. domestica</i>
Asian group	<i>P. salicina</i>	Native in the Basin of Yangtze River
	<i>P. simonii</i>	No wild form, only cultivated
	<i>P. ussuriensis</i>	Along Ussuri River
American group	<i>P. subcordata</i>	Native of California and Oregon
	<i>P. mexicana</i>	South-western Kentucky to Western Tennessee to Oklahoma and Mexico
	<i>P. rivularis</i>	Native in Texas
	<i>P. maritima</i>	From Brunswick to Virginia
	<i>P. americana</i>	From Massachusetts to Georgia to near the Gulf of Mexico and to the west
	<i>P. nigra</i>	From New Brunswick to Northern Ohio
	<i>P. angustifolia</i>	From Delaware to Florida and Texas
	<i>P. hortulana</i>	Native in Central Kentucky and Tennessee, to Iowa and Oklahoma
<i>P. munsoniana</i>	From Kentucky to Kansas and Texas	

2.3.5. Geographic origin and natural distribution of *P. avium* and *P. cerasus*

Watkins (1976) suggests that the first diploid *Prunus* species arose in central Asia, and that species in the section *Cerasus* which includes sweet, sour and ground cherry, were early derivatives of this ancestral *Prunus*. The *Cerasus* cherries developed to the west of the central Asian subgenus *Cerasus*' centre of origin while most other *Cerasus* species evolved to the east.

Hedrick (1915) described the geographic range of wild sweet cherry as all of mainland Europe well into the Southern U.S.S.R. and as far east as Northern India, with the greatest prevalence between the Caspian sea and the Black sea. In contrast, the ground cherry centre of origin is Western and Central Asia (Watkins, 1976).

It is reported that sweet cherries (*Prunus avium*) were brought in 74 B.C by the Roman General Lucullus from Cerasunt on the Black Sea to Rome, and from there spread to Germany and Britain.

Sweet cherries (mazzard) have been grown from Southern Russia, north of the Caucasian mountains to the north of France for a long time. *Prunus fruticosa* Pall., the ground cherry, has a wider area of distribution, which overlaps with the centre of wild cherry, thus giving new hybrids as sour cherries. The sour cherry is native in the Carpathian Basin. Domestication and cultivation has resulted in

some ecotypes of sweet and sour, or ground cherries in the various areas of Europe, and partly in Asia. Several sweet and sour types are adapted to harsh winter conditions (Iezzoni et al., 1990; Faust and Surányi, 1997).

Although cultivated cherries are ubiquitous in the temperate zone, there has been little effort to take them further south into subtropical regions. There are those cultivars which require low-chilling among the cherry genotypes, although the existing high quality cherry cultivars all have high chilling requirements. Commercial production of sweet cherries is limited by rain fall during the ripening period, which causes cracking of Bigarreau-type sweet cherries and subsequent brown-rot infection, which destroys the value of the fruit.

Sour cherries are not subject to cracking, nevertheless, they are also better adapted to cool climates. Most of the world cherry production is in Europe, its native home.

Duke cherries are hybrids between sweet and sour cherry varieties.

Wild and cultivated species are useful in breeding and cultivation:

<i>P. avium</i> L.	native of Eurasia
<i>P. cerasus</i> L.	a hybrid between <i>P. avium</i> and <i>P. fruticosa</i>
<i>P. fruticosa</i> Pall.	grows in Southeast Asia and Central and Western Europe
<i>P. mahaleb</i> L.	grows in Southern and Central Europe and Asia Minor
<i>P. pseudocerasus</i> L.	originated in the North China
<i>P. tomentosa</i> Thunb.	native in the Chinese provinces and Eastern Tibet

Furthermore, there exist American and Asian ecotypes:

- *P. capuli* L. Mexican cherry
- *P. japonica* Thunb.
- *P. maackii* Rupr.
- *P. pumila* L.
- *P. serrulata* Lindl.

2.4. Reproduction biology of the genus *Prunus*

2.4.1. Sexual reproduction.

This genus is exceptional in the *Rosaceae* family - representing the evolutionally most advanced taxon - with a pistil reduced to one carpel only. In the pistil, there are regularly two ovules but in the majority of cases only one grows to seed. The rate of two (or even more) seeds per stone are sometimes typical for particular varieties in Pomaceous pistils but are rare in *Prunus*. The androeceum, with its three whorls of stamina with regular anthers does not show much difference from the average of the family. Seeds of pollinated fruits with embryos issued from zygotes as a product of fused sexual cells (gametes) are the main form of reproduction, even though interspecific hybrids with generative sterility and many cultivars are able to produce tillers. There is no indication of apogamy or parthenogenesis, neither of parthenocary, except in some varieties with signs of aborted embryos as a result of selection for extra

early ripening. In that case, however, *in vitro* rescue of excised embryos may secure the survival of the offspring. The genetic dynamics of the species are secured by a high rate of outbreeding conditioned by a polyallelic system of autoincompatibility (2.4.2). The seeds are tightly closed in the stone, i.e., the lignified endocarp of the fruit. For germination, however, the seeds need to be stratified, i.e., exposed to temperatures below 10°C for some weeks or months, practically over the winter to start germination, moreover, excised seedlings from ripe seeds also need some “chilling” in order to develop normally, i.e. to produce elongated shoots axes. The same holds true for the excised, underdeveloped embryos rescued for breeding purposes.

In almond, self-incompatibility is controlled by different alleles of a gametophytic self incompatibility gene (Kester and Asay, 1975; Crossa-Raynaud and Grasselly, 1985; Socias i Company and Felipe, 1988). Self-fertility genes have been found in almond and related species. Recently, 17 additional self-fertile genotypes have been identified in wild almond populations in Italy (Reina et al., 1985).

Prunus persica is self-fertile. However, pollen sterility in *P. persica* could be useful for interspecific hybridisation.

In apricot, most Central Asian cultivars are self-incompatible, while most European cultivars are self-compatible (Mehlenbacher et al., 1991).

Most sweet cherry cultivars presently being grown are self-incompatible. Self-incompatibility in sweet cherry was first identified by East and Mangelsdorf (1925) and later determined to be of the monofactorial gametophytic type with multiple allelic S locus (Lewis, 1948).

Self-fertility in sweet cherry has been obtained through X-ray radiation applied to flower buds at the pollen mother cell stage (Lewis, 1948; Lewis and Crowe, 1954) and by spontaneously occurring mutations (Lewis, 1951).

2.4.2. The mating system of most cultivated *Prunus* species

The mating system of most cultivated *Prunus* species is determined by the clearly defined system of auto-incompatibility, which is inherently combined with inter-incompatibility. However, the high number (20-40) of known alleles of the single (Sx) locus with gametophytic determination allows little chance of meeting incompatible mates amongst the varieties cultivated. Those incompatible combinations are registered according to experimental proofs accumulated during the last, nearly seventy years since the phenomenon has been detected. Auto-incompatibility is expressed at different degrees between total, intermediate and scarcely identified cases. The apparent lack of such a mechanism is found in peach, although male sterility occurs at a relatively high frequency, e.g., the cultivar J.H. Hale, and in some plums, e.g., the cvs Tuleu gras, Pitestan and Carpentin (Silbereisen et al., 1996). The evolutionary role of male sterility is highly analogous to that of incompatibility. As a general tendency of the domestication process, the increased rate of self-fertility is derived from the selection pressure for high and regular yields in crops grown for their generative organs. This can be seen in the *Prunus* species as many, mainly recently developed, varieties are self-fertile. In modern times, self-fertility has been consciously favoured. Another condition of self-fertility is polyploidy appearing on the margin of the spreading species like the European plum and sour cherry as amphiploids of interspecific hybrids in which activity of the S alleles is impaired. No doubt that some of those clones are also tillering spontaneously. Conditions of cultivation, introduction to new habitats included, are similar to the marginal areas of a species where rare mutations enjoy better chances to survive. All those reasons enhance the chances of self-fertile genotypes. Some exceptions in European plum and sour cherry prove that auto-incompatibility did not disappear entirely with amphiploidy, so a conscious effort in the research for high productivity gave rise to new, self-fertile sour cherry cultivars.

Search for radiation-induced mutants in cherry populations has spotted the Sf allele, which proved to be dominant in relation to the rest of the sterility alleles. This phenomena is employed in breeding programmes in order to produce new self-fertile cherry cultivars. The first self-fertile sweet cherry cultivar was released from a breeding program in 1968 and named Stella (Lapins, 1971). It was the result of a cross between Lambert and JI 2420. The cross was made in 1956. JI 2420 came from the John Innes Institute in the UK and was the result of a cross between Emperor Francis and irradiated pollen from Napoleon. At the moment all self-fertile cultivars have Stella in its pedigree somewhere. The John Innes Institute had a couple of other selections that were self-fertile but they have not yet made it into a named cultivar.

Bees play a major role as pollinating agents, as the pollen of *Prunus* species cannot be carried by wind and even self-pollination requires the mechanical intervention of insects.

2.4.3. Natural vegetative multiplication

Natural vegetative multiplication is rather exceptional in the genus of *Prunus*, but all subgenera have members which build up extended colonies by tillering, and some successful cultivars have been maintained by tillers since ancient times, e.g., European (hexaploid) plums in the NE-Hungary (in the riverside of the Tisza river) and there are clones of semi-wild cultigens, blackthorn and sour cherry. Most of the existing cultivars are, however, multiplied by grafting and trading, except, some old varieties, such as the sour cherry variety Cigánymeggy (Hungary) and Oblacinska (Former Yugoslavia). In the group of almonds the only tillering wild species, *P. tenella*, is eligible as a potentially dwarfing stock.

More attempts have been invested into the vegetative propagation of *Prunus* rootstocks. As very few are inclined to develop tillers spontaneously, the tools of micropropagation *in vitro* gained particularly high interest, for example, in the rapid multiplication of GF 677. In fact, millions of plants are produced world-wide by *in vitro* techniques (Rosati and de Paoli, 1992). The production of self-rooted plantlets by green cuttings under a mist curtain seems to be less favoured mainly because of the questionable value of the self-rooted trees and/or the low efficiency of the technique. Grafting techniques, on the other hand, became routine several centuries ago. In addition, some stocks are propagated with cuttings.

2.5. Crossability

2.5.1. Interspecific and Intergeneric Hybrids

Interspecific (and intergeneric) relations in *Prunus* are not clear, perhaps due to the widespread presence of auto-incompatibility and the relative fertility of interspecific hybrids. The prolonged time period for flowering in the *Prunus* species and even within varieties of one species, substantially influences the possibility of mutual pollination between different cultivars, as well as different species. This is due to the different phases in flowering during the blooming season of the cultivated *Prunus* species.

The physiological or ecological diversity of the species caused sufficient isolation of their individual habitat. Consequently, they were scarcely sympatric in their natural environment, whereas, some *Prunus* species were grown, regularly, in home gardens if not in larger orchards. Interspecific barriers did not develop during natural evolution, but by the appearance of cultigenous hybrids, which triggered their development from the first steps of domestication up to the limits set by taxonomic divergence. Although the cherries are perhaps the most distant from the rest of the species, we find bridging species between plums and cherries as documented for *P. salicina*. Less difficult seems to be the

gene flow between plum-apricot-peach and almond as documented by the list of successful interspecific crosses (Table 1).

Table 1 - Interspecific hybrids with *Prunus persica*

<i>P. amygdalus</i>	x <i>P. persica</i>
	x (<i>P. amygdalus</i> x <i>P. davidiana</i>)
<i>P. armeniaca</i>	x <i>P. davidiana</i>
	x <i>P. persica</i>
<i>P. besseyi</i>	x <i>P. persica</i>
<i>P. cerasus</i>	x <i>P. persica</i>
<i>P. hortulana</i>	x <i>P. persica</i>
<i>P. nana</i>	x <i>P. persica</i>
<i>P. persica</i>	x <i>P. amygdalus</i>
	x <i>P. davidiana</i>
	x <i>P. cerasifera</i> var. <i>divaricata</i>
	x cherry (sps?)
	x <i>P. kansuensis</i>
	x <i>P. mira</i>
	x <i>P. nana</i>
	x <i>P. besseyi</i>
	x <i>P. salicina</i>
x <i>P. spinosa</i>	
<i>P. salicina</i>	x <i>P. persica</i>
<i>P. spinosa</i>	x <i>P. persica</i>
<i>P. tenella</i>	x <i>P. davidiana</i>
	x <i>P. persica</i>

Source: after Janick and Moore, 1975

All the species mentioned have been intercrossed with various degrees of difficulty, and grafted on each other within reasonable limits, which is proof of their genetic and physiological affinities. The use of rootstocks enlarges, dramatically, the possibilities of occupying ecological niches previously inaccessible with species on their own roots.

Hybridisation readily takes place between *Prunus amygdalus* and *Prunus persica* (Kester and Asay, 1975, 1988). Naturally interspecific hybrid rootstocks, 'GF 667', are common, where the two species are grown together.

North-American species and their interspecific hybrids, created between 1907 and 1965, represent a distinct group of cultivated *Prunus* species, the "cherry plums" (different from the species *P. cerasifera*, the cherry plum in the traditional sense). They are derived essentially from *P. besseyi* and *P.*

pumila, with the western and the eastern sand cherry as a common parent (Janick and Moore, 1975) (Table 2).

Table 2 - Hybrids of the sand cherries (*P. besseyi* and *P. pumila*) with other species

Sand Cherry	x <i>P. americana</i>
Sand Cherry	x <i>P. salicina</i>
Sand Cherry	x <i>P. salicina</i>
Sand Cherry	x <i>P. simoni</i>
Sand Cherry	x <i>P. armeniaca</i>
Sand Cherry	x <i>P. persica</i>

Source: Janick and Moore, 1975

It is remarkable that peach (*P. persica*) is one of the most flexible species of *Prunus* regarding its use in interspecific crosses for breeding purposes. The documented products of these breeding efforts are divided into two distinct groups: Hybrids mostly fertile (A) and mostly sterile (B). A complicated polyhybrid background is surmised in most cases from taxa *P. davidiana* (d), *ferganensis* (f), *kansuensis* (k), *mira* (m) and *persica* (p) according to Scorza and Okie (1990) and Janick and Moore (1996) (Table 3). In group (A), we may consider the hybrid products as potentially new fruits, i.e. distinct commodities, as it happened with the sand cherry derivatives in the Midwest of the United States.

Table 3 - *Prunus* species reported as hybrids between peach and peach species

Species		Hybrid	Common name	Origin
<i>P. amygdalus</i>	(A)	d.m.p.	almond	SW Asia
<i>P. davidiana</i>	(A)	k.p.	mountain peach, shan tao	N China
<i>P. ferganensis</i>	(A)	p.	xinjiang tao	NE China, S Russia
<i>P. kansuensis</i>	(A)	d.p.	wild peach, kansu tao	NW China
<i>P. mira</i>	(A)	p.	Tibetan peach, xizang tao, smooth-pit	W China-Himalayas
<i>P. persica</i>	(A)	d.f.k.m.	peach, maotao	China
<i>P. americana</i>	(B)	p.	American plum	USA
<i>P. armeniaca</i>	(B)	d.p.	Apricot	Asia
<i>P. besseyi</i>	(B)	d.p.	western sand cherry	N USA, Canada
<i>P. brigantina</i>	(B)	p.	Briancon apricot	France
<i>P. cerasifera</i>	(B)	d.p.	myrabolan plum	W Asia
<i>P. cerasus</i>	(B)	p.	sour cherry	W Asia, SE Europe
<i>P. domestica</i>	(B)	p.	European plum	W Asia, Europe
<i>P. hortulana</i>	(B)	p.	wild plum	C USA
<i>P. japonica</i>	(B)	p.	Chinese bush cherry, Korean b.c.	China
Species		Hybrid	Common name	Origin
<i>P. nigra</i>	(B)	p.	Canadian plum	N USA, Canada
<i>P. pumila</i>	(B)	p.	eastern sand cherry	N USA
<i>P. salicina</i>	(B)	f.p.	Japanese plum	China
<i>P. simmonii</i>	(B)	p.	Simon's plum	N China

<i>P. spinosa</i>	(B)	p.	sloe or blackthorn	Europe, W Asia, N Africa
<i>P. tenella = nana</i>	(B)	d.p.	Siberian almond	SE Europe, W Asia
<i>P. tomentosa</i>	(B)	p.	Chinese bush cherry, Manchu cherry	N&W China, Japan
<i>P. virginiana</i>	(B)	p.	choke cherry	N USA, Canada

(A) Closely related to peach producing fertile hybrids

(B) Hybrids mostly sterile. The codes of species used as parent in the ancestry:

P. davidiana (d), *ferganensis* (f), *kansuensis* (k), *mira* (m) and *persica* (p)

The only valid example of commercially recommended interspecific pollinations is between sweet and sour cherry (Nyéki and Soltész, 1996). As parthenocarpy, understood as seedless fruit, does not exist in *Prunus*, it seems obvious that seed abortion might have little chance in fruit production, however, some extra early ripening cherry and peach varieties are used to develop unviable seeds. It was proved that the excision of the embryos before the fruit have ripened facilitates the rescue of plantlets under *in vitro* conditions. Thus an efficacious technique has been developed for use by breeders in combining genes of those extra early varieties, e.g., Bailey and Hough.

Because of the ease of natural hybridisation of *P. fruticosa* with *P. cerasus* and *P. avium*, some *P. fruticosa* rootstocks under testing may be interspecific hybrids.

Prunus tomentosa has been hybridised with cherry (Fisher and Schmidt, 1938; Noznikov, 1951). *Prunus salicina* hybridizes easily with *P. simonii*, *P. armeniaca*, and American plum species.

No difficulties have been reported in intercrossing *P. armeniaca*, *P. sibirica*, *P. mandshurica* and *P. mume*, although not all combinations have been attempted. *P. x dasycarpa* has been backcrossed to both *P. cerasifera* and *P. armeniaca*; crosses to the plum parent are generally easier.

Results to date indicate that crosses between true apricot species (*P. armeniaca*, *P. mandshurica*, *P. sibirica* and *P. mume*) are successful when made in either direction and resulting hybrids are viable and fertile.

A large number of crosses between various plum and apricot species have been reported. Listed in order of flowering date, they are *P. salicina* Lindl., *P. X dasycarpa*, *P. cerasifera* Ehrh., *P. domestica* L., *P. besseyi* Bailey, and *P. maritima* Marsh. The initial cross is generally more successful when plums are used as the female parent. *P. cerasifera* x *P. armeniaca* produced hybrids resembling the natural interspecific hybrid species *P. X dasycarpa*.

Hybrids of the Asian plum species *P. salicina* with *P. armeniaca* have also been generated with little difficulty. Fertility of the hybrids varies; pollen fertility is generally quite low.

Several authors also report successful hybridisation of the hexaploid plum *P. domestica* with apricot. Resulting hybrids are tetraploid.

The beach plum, *P. maritima* has also been hybridised successfully with common apricot. More distant hybrids of apricots with peach and almond have been reported. These crosses are quite difficult to make and the resulting hybrids are often weak and sterile. The incorporation of genes from *P. persica* could conceivably greatly expand the areas in which apricots could be grown.

2.5.2. *Introgression into Wild Relatives*

The introgression between cultivated and wild species is scarcely documented. There is no doubt concerning the physical possibility. Escapes of cultivated varieties are frequently found in woods, pastures, abandoned orchards, ruderal, suburban, and marginal areas. Intercrosses with really wild populations have very little chance, as blackthorn, hedge cherry and dwarf almond (*P. tenella*) are extremely different in morphology, as well as in adaptation, i.e. eventual hybrids could only survive in a much protected environment. Cherries may have more chances as far as introgression into the wild populations is concerned. It is worthwhile to consider the escapes of varieties and species introduced as rootstocks to nurseries and grown out from the roots and stumps of destroyed grafts in abandoned orchards. That is how a high diversity of cherry plums have been naturalised recently. As a result, the cherry plum has become much more tolerant than the European plum and apricot to the destructive effect of Plum Pox Virus (PPV). Escaped rootstock varieties and spontaneous hybrids of ancient, as well as, recently introduced varieties are a general phenomena found in neglected orchards, and escapes of no immediate relation to fruits growing in the area are found. For example, *P. serotina*, *P. mahaleb*, *P. padus*, bitter almonds.

In Central Europe, the possibility of introgression is much more limited to the Near East, Caucasus, Iran, Central Asia and the Chinese subcontinent, where a huge wealth of intermediate and semi-cultivated forms reside.

Section III - Domestication of *Prunus* species

3.1. Breeding of *Prunus*

One of the obvious reasons for the abundant domestication of the *Prunus* species might have been the coincidence between the centre of variability of *Prunus* and the site of human evolution and/or of the first ancient high civilisations of human history. The easily fossilised stone of the fruit proved that fruit of considerable size existed long before the appearance of man. Plums “offered themselves” to man to be domesticated. According to ecological arguments, it is highly probable that the today despised species, e.g., blackthorn (*P. spinosa*) followed men as a “secondary crop” which is reflected in its occurrence as a witness of the ancient Neolithic culture on the outskirts of the villages, roadsides and pastures as hedges. The ancestors of that tetraploid species are unknown. It survived adversities of severe pasturage but benefited from deforestation during the spreading of primitive agriculture in the Near East and Europe, where its more vigorous relative, the favoured fruit tree, the diploid cherry plum (*P. cerasifera*) presented a permanent temptation for crossbreeding. The appearance of the European plum (*P. domestica* and *insititia* included) was not an unique and endemic event in the history of the Eurasian region. The hexaploid, (amphiploid) species has been reproduced at several instances by purposeful breeding, according to the model of bread wheat, triticale, tobacco, oilseed rape, garden strawberry, and other cultivated species, first perhaps by Rybin, a disciple of Vavilov in the 1930s. Since ancient and medieval times, the European plum made an important carrier, first owing to its ability of producing tillers as its alleged ancestor, the blackthorn also did, and secondly, because it became naturalised in mesophytic marginal cultivated areas and some river flats (e.g., of Felső-Tisza). As the most important fruit and almost staple food, it served the well being of poor people for centuries. However, later on, it became one of the first horticultural products to be exported and became of this, was seen as a symbol of wealth (as the greater number of plum trees on the manor of a member of the gentry, the more wealthy he was). The distilled drink achieved its fame as the national drink in S-E Europe, replacing gin. Recently, the fate of the European plum has been severely impaired, by the Plum Pox Virus, which was identified during the first part of the 20th century.

In the rich choice of plums, a host of species originating from East Asia and North America are diploid. These species have been inter-crossed with the cherry plum with considerable success. As a result, in the last few decades there has been an impetus of the so-called Japanese Plums. The first documented attempts are due to Luther Burbank, a Californian breeder at the end of the 19th century. Those interspecific hybrids, however, well represented in the list of cultivars, only represent a small fragment of the huge gene reserves of the Northern Hemisphere. As a source of precious genes, especially for resistance and special qualities lacking from the traditional European plum, these varieties are to be kept in mind.

3.2. Conservation of *Prunus* Genetic Resources

The International Plant Genetic Resources Institute (IPGRI), formerly known as the International Board for Plant Genetic Resources (IBPGR) has elaborated a descriptor list for plum, peach, cherry and apricot (IBPGR 1984a,b,c, 1995) and developed recommendations for the safe movement of germplasm of stone fruits (Diekmann and Putter, 1996).

The European Information Platform on Crop Genetic Resources has been established under the umbrella of the European Co-operative Programme for Crop Genetic Resources Networks (ECP/GR) to facilitate access to information about genetic resources conserved in genebanks throughout the Region. The European *Prunus* database has been maintained by Dr. Anne Zanetto at the “Institut National de la Recherche Agronomique” (INRA) in Bordeaux, France, under the initiative of the European Co-operative Programme for Crop Genetic Resources Networks (ECP/GR) since 1994. The database includes, in 26 European countries, the collections of all *Prunus* species, cultivated stone fruit and their related species (even the wild ones). The database is comprised of 19 passport data from the IPGRI/FAO Multicrop descriptors list, 13 descriptors common for all the different species and 3 to 7 specific descriptors depending on the species of the accession. These descriptors are mainly morphological. The possibility of including more agronomic or physiological descriptors is under consideration by the ECP/GR *Prunus* Working Group. The database has been supported for three years by the European Union in the “European Programme on the conservation, characterisation, collection and utilisation of genetic resources in agriculture”, under the title “International Network on *Prunus* genetic resources” (GENRES61). In addition, there are gene banks in China and Japan.

3.3. Synecology

In Europe, some wild, native and escape species of *P. nana*, *P. avium*, *P. fruticosa*, *P. mahaleb* and *P. spinosa* can be found in natural and cultivated forests or ruderals.

3.4. Interaction with Pathogens

Rosaceae, in general, and *Prunus* species, in particular, are prone, in varying degrees, to infections by a range of pathogens, e.g. fungi such as *Monilia laxa*, *Taphrina deformans*, bacteria, such as *Pseudomonas*, and *Xanthomonas*, viruses, such as PPV, PNRSV and PDV and phytoplasmas such as European Stone Fruit Yellows (ESFY) (<http://www.boku.ac.at/pbiotech/phytopath>).

The main problems associated with apricot growing include: die-back or apoplexy, sensitivity to viruses, frost damage in winter and spring, fungi cankers and alternate bearing.

In recent years, a viral pathogen became the major threat to stone fruit cultivations in large areas of Central and Southern Europe and other Mediterranean countries. This pathogen was responsible for considerable economic losses and reduction of production areas. The Plum Pox Virus (PPV), causal agent of Sharka disease and a member of the potyvirus family, was classified by US and EC plant quarantine agencies as the most important pathogen in apricots, plums and peaches (the only plant pathogen for which an APHIS plan exists (Scorza, 1991). Sharka infection data from Spain, Greece, France and Italy clearly demonstrates the economic consequences of this threat (COST 88 Plum Pox Virus Workshop -Potyvirus Group, Valencia June 1993), as apricot cultures are increasingly being replaced. Apricot appears to be the most sensitive stone fruit towards infection with PPV. Apricot production was practically erased in the late 70s in some valleys of Northern Italy, e.g., Vintschgau (Eynard et al., 1991), and is seriously threatened in some Austrian valleys, e.g. Wachau (Pieber, pers. comm). After its appearance in the South American Continent (Herrera et al., 1997) in 1999, it has been confirmed for the first time in the US (<http://aphis.usda.gov/lpa/press/1999/10/plumpox.txt>). This prompted Canada to close the entry of *Prunus* material from the US (<http://www.cfia-acia.agr.ca/english/corpaffr/newsrelease/19991122e.shtml>).

Considering the severity of the disease, the difficulty to control its spread, and the lack of resistant cultivars, the necessity of resistant cultivars is evident and a straight-forward strategy is required. In fact there are no species resistant to Plum Pox Virus among the species sexually compatible to crop cultivars. This means it is not possible to obtain resistant cultivars by conventional hybridisation.

The information concerning the interrelation of *Prunus* species gives an opportunity of considering their pathosystems. Most pathogens and pests have developed along evolutionary pathways in parallel with the domestication and evolution of new species and hybrids. Because of geographical continuity, most species coming from the East carried their parasites freely. One of the best examples is the green peach aphid, *Myzus persicae*, which proved its fidelity to the peach tree in spite of being polyphagous; neither related species substituted the peach as a primary host. It is remarkable that even though the peach was one of the last oriental species to arrive in Europe, the green peach aphid became one of the most efficient vectors of viral diseases in Northern Europe. On the contrary, a pathogen *Taphrina deformans* did not harm either of the relatives of peach. Although, another adapted disease, *Polystigma rubrum* kept to the European plum (and blackthorn) as host, in spite of the permanent sympatric presence of relatives of the *Prunus* genus. Different susceptibilities to other diseases and pests indicates the existence of genetic resistance in spite of the possibly, small genetic divergence, e.g. the reduced proliferation of aphids on apricots in relation to peach and plum.

The increasing threat of stone fruit production in Mediterranean countries by phytoplasma diseases has been recognised in recent years. Although severe decline of European stone fruits was reported as early as 1924 on apricots in France and in 1933 on Japanese plums, in Italy it was only in 1973 that their phytoplasma aetiology was discovered. At that time, phytoplasmas were called mycoplasma-like organisms (MLOs). As different *Prunus* species were affected, different disease names were given: apricot chlorotic leaf roll (ACLR) on apricots, plum leptonecrosis (PLN) on Japanese plums, peach yellows, peach rosette and peach vein clearing (PVC) on peach and several other decline diseases on European plum, almond and flowering cherry. *Prunus* rootstocks are also severely affected by similar disorders. Common symptoms are yellowing and leaf roll in summer, off-season growth in winter, die-back and a more or less rapid decline. Up to now these diseases have been restricted to the southern half of Europe with their northern border in Germany. In the past few decades they have been of increasing economic importance, e.g. ACLR and PLN are especially devastating for apricots and Japanese plums. Molecular analysis of the pathogen revealed that only one type of phytoplasma, the European stone fruit yellows (ESFY) phytoplasma, is associated with all these diseases (Jarausch et al., 2000). ESFY phytoplasmas are genetically different from phytoplasmas infecting *Prunus* species in North America. ESFY phytoplasmas are classified as quarantine organisms by European legislation (Laimer da Câmara Machado et al., 2001; Heinrich et al., 2001). Upon experimental inoculation, apricot, peach and Japanese plum are the most susceptible stone fruits whereas European plum and almond are more tolerant and cherries appear to be resistant (Jarausch et al., 2000).

Section IV - References

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