



Unlocking Plum Genetic Potential: Where Are We At?

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Abstract: Plums are a large group of closely related stone fruit species and hybrids of worldwide economic importance and diffusion. This review deals with the main aspects concerning plum agrobiodiversity and its relationship with current and potential contributions offered by breeding in enhancing plum varieties. The most recent breeding achievements are revised according to updated information proceeding from relevant scientific reports and official inventories of plum genetic resources. A special emphasis has been given to the potential sources of genetic traits of interest for breeding programs as well as to the need for efficient and coordinated efforts aimed at efficaciously preserving the rich and underexploited extant plum agrobiodiversity. The specific objective of this review was to: (i) analyze and possibly evaluate the degree of biodiversity existing in the cultivated plum germplasm, (ii) examine the set of traits of prominent agronomic and pomological interest currently targeted by the breeders, and (iii) determine how and to what extent this germplasm was appropriately exploited in breeding programs or could represent concrete prospects for the future.

Keywords: agrobiodiversity; breeding; interspecific plum hybrids; *Prunus domestica*; *Prunus salicina*



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1. Introduction

Plums include a large and diverse group of closely related *Prunus* species of the *Rosaceae* family, having a common putative ancestor originated about 31 Myr [1,2], and presenting a wide range of variation in terms of fruit size and shape, flavor, aroma, texture, and color, greater than in any other fruit crop [3], together with a large range of potential utilizations, for direct consumption and processing. Although this plurality within “plums”, has only two types, the hexaploid ($2n = 6x = 48$) European plums (*Prunus domestica* L.) and the diploid ($2n = 2x = 16$) Japanese plums (*Prunus salicina* Lindl.), are extensively cultivated worldwide. There is a distinction based on fruit use which distinguishes species for fresh fruit consumption, properly called “plums”, from others that are dried, shipping fruits, known as prunes or dried plums, corresponding to *P. salicina* and hybrids, and *P. domestica*, respectively.

P. domestica and *P. salicina* have a long history of cultivation (4000–6000 yrs) [4] in Europe and Asia, respectively, and are today the most globally cultivated plum species on which the current plum industry is based.

Here we describe the overall genetic and varietal aspects influencing plum diversity and review the implications and opportunities for present and future breeding strategies in relation to these.

1.1. Plum Production and Market Aspects

Among stone fruits world production, plums rank second after peach and nectarines and before cherries. Globally, Japanese plum production is greater than that of the European plum. As of 2019, FAO records just over 2,700,000 hectares of plum trees (including

European and Japanese plum and hybrids) in the world and a total production of about 12,600,000 tons, with an increase of 20% in the last decade. China is the leading producing country (77% and 56% of world area harvested and production, respectively), followed by Romania, Serbia, Chile, Iran, USA, Turkey, Italy, France, Ukraine and Spain. Chile is the largest plum exporter in the world, mostly (\approx two-thirds) to China, the United States and Brazil. Plums are the most imported stone fruit in Europe, and Germany is the largest EU destination market for fresh imported plums. Romania and Serbia are the largest plum producers in Europe, but their production is mainly destined for internal consumption and for processing (prunes and spirit), so a very small quantity are exported. Spain and Italy remain Europe's most important suppliers of fresh plums to neighboring markets, though their plum exports have been declining in recent years [5,6]. South Africa is the largest non-European supplier to EU countries, but Chile, Moldova and Serbia grew the most in plums for export by volume to Europe [7]. Production in the United States is concentrated in California, chiefly in the Sacramento Valley, which is the world leader in dried plum (prune) production, even if, in comparison with the 2001 data, both the surface and the production have now more than halved, showing a continuous decreasing trend. U.S. exports by value (MIO USD) in the last four years has averaged 134 and 57, for prunes and plums, respectively [8].

Plums are highly appreciated by consumers for their attractiveness, contrasted taste and juiciness, the wide range of flavor intensity, aroma, texture, color, shape, and size [9–12], but also recently for their nutraceutical properties and high antioxidant content [13–16]. The nutritional properties of several European and Japanese cultivars are reported by Wolf et al. [17]. Additionally, a recent systematic review on the health effects of plums showed that plum consumption is associated with improved cognitive function, bone health parameters and cardiovascular risk factors [18]. However, the annual per capita consumption of plums remains, on a world basis, lower than for that of peaches (1.8 and 2 kg, respectively) although it differs significantly from one country to another. Serbia has the highest per capita consumption (27 kg), followed by Bosnia and Herzegovina (21.2), Montenegro (15.7), and Romania (13.9 kg) [7].

1.2. The Rationale for Plum Breeding

At present, the main cultivated plums, not unlike a very large part of the cultivated plants, show a relatively limited intra-specific genetic variability [19], although broader than other commercial *Prunus* species, due to introgression of genes from related species [20]. Recent genetic studies using different molecular approaches has indicated that the cultivated diploid plums have about the same level of diversity as almonds, but more diversity than cultivated peach or apricot [21].

This limited variability has to be related to several causes such as the process of domestication combined with clonal propagation, the use by modern breeders of an often-reduced number of parents of similar origin, as well as a process of standardization/homogenization for agronomic, processing, and commercial reasons which reveal a relatively broad genetic bottleneck [4,22–24]. As a result, the progressive loss of old traditional cultivars and the increasing narrowing of the genetic base is occurring, with the consequence of inbreeding depression phenomena that undermines the potential for future breeding progress [25,26], and increases vulnerability to pests, diseases, and environmental change. In this context, plum germplasm accessions (old traditional cultivars, landraces, related or wild progenitor species, especially in the original centers of diversity), which may have been less subjected to artificial selection pressures [27], can play a crucial role in the gene-pool reservoir which might be exploited for breeding purposes, especially in areas of fruit quality, disease resistance, climatic adaptability, and new rootstocks selection [28–33]. Considering its present and future strategic role, this germplasm deserves, overall, special attention and coordinated efforts of conservation [34], evaluation and utilization for breeding purposes [35] by both conventional and innovative (genomic) approaches [36]. A special concern is reflected in specific situations where most of the production is from a few cultivars or even,

as in California, from a single cultivar, the “Improved French”, with increased risks of vulnerability of the entire production system [37].

For these reasons there is a growing and urgent need to preserve as much of the extant *Prunus* diversity as possible and to develop new viable plum cultivars, well adapted to different cultural conditions and with favorable qualitative and nutritional aspects, as is expected from the breeding programs underway in different countries.

The specific objective of this review is to: (i) analyze and possibly evaluate the degree of biodiversity existing in the cultivated plum germplasm, (ii) examine the set of traits of prominent agronomic and pomological interest currently targeted by the breeders, and (iii) determine how and to what extent this germplasm was appropriately exploited in breeding programs or could represent concrete prospects for the future.

2. *Prunus* Taxonomy, Species Identification and Diversity

Plums have been considered a link between the major subgenera in the genus *Prunus* with high diversity and heterogeneity [4]. *Prunus* is a complex, cosmopolitan genus of the *Rosaceae* family, sub-family *Amygdaloideae* (=Prunoideae), originated in eastern Asia about 61 Myr, whose major diversification, including hybridization events, may have been triggered by the global warming period of the early Eocene [1]. It encompasses all the stone fruit species of worldwide diffusion and paramount economic importance, together with several wild species, accounting for about 250–400 deciduous and evergreen trees and shrub species. These species, many of which are cultivated for their edible fruit and/or for ornamental purposes [38], share common typical reproductive organs (superior ovary position and a drupe as its fruit, containing a hard endocarp, i.e., the stone) and show an essential common genome where the base chromosome number is 8 [39].

The genus is subdivided into five subgenera: (i) *Amygdalus*, which includes almond (*P. dulcis* D.A. Webb), and peach (*P. persica* (L.) Batsch); (ii) *Cerasus*, the sweet (*P. avium* L.) and sour (*P. cerasus* L.) cherries; and (iii) *Prunus*, which consists of three types: *Armeniaca* (Lam.) Koch. (*Apricots*), *Prunocerasus* Koehne (North American plums), and *Prunus* (Eurasian plums) [40], the latter clearly distinct from the other sections [41,42]. Eurasian plums include the hexaploid European (syn. French) (*P. domestica* L.) and the diploid Japanese (or Asian) plums (*P. salicina* Lindl.).

While *Prunus* and *Amygdalus* were considered by Watkins [43] as a single gene pool, on the other hand the remaining two subgenera, *Padus* (deciduous bird-cherries) and *Laurocerasus* (evergreen laurel-cherries) are considered more isolated within the genus *Prunus* [44].

Although there are reproductive barriers between diploid and hexaploid plum species, sexual compatibility is frequent within the members of the same subgenus, and hybridization between species belonging to *Amygdalus* and *Prunus* subgenera is also possible [39].

Due to this complexity and recurrent hybridizations and/or allopolyploidy phenomena, taxonomy has been controversial until recent times [3,44], and phylogenetic studies, both with nuclear and chloroplast approaches, have recently revealed an intricate evolutionary history of the genus along with close, but conflicting, relationships among and within subgenera [1,42,45–47].

However, the recent availability of whole-genome sequences (WGSs) has paved the way for a better understanding of the genetics of this large group of species belonging to the genus *Prunus* [39] (e.g., *Prunus salicina* genomes from ‘Sanyueli’ and ‘Zhongli’, *Prunus domestica* ‘Honey Sweet’, and *Prunus mira*).

Apart from the two major Eurasian fruit species (*P. domestica* and *P. salicina*), several minor edible plum species or pomological groups, often small-fruited, of different origin and horticultural relevance as scion or rootstocks, are, inter alia, the myrobalan plum, or “Cherry plum” (*P. cerasifera* Ehrh.) extensively used as a rootstock for plums, e.g., ‘Ishtarà’, ‘Jaspi’, ‘Julior’, ‘Citation’, ‘Marianna’ [31], the blackthorn, or sloe, (*P. spinosa*), mirabelles, bullaces, damsons, greengages and ‘St. Julien’ (*P. insititia* L.) along with Asian species such as *P. simonii* Carr. and native American species such as *P. americana* Marsh.,

P. angustifolia Marsh., *P. mexicana* Wats., *P. nigra* Ait. and *P. hortulana* Bailey. The major distinctive characteristics and uses of the species pertaining to these plum pomological groups have been thoroughly revised by Faust and Suranyi [3], Topp et al. [4], Okie [48] and by Gaši et al. [49] and will not be further discussed here. Molecular studies a different and complex origin [50] for most of them, and archaeobotanical evidence and citations reported in historical and literary texts [3,51–53], underpin the hypothesis of a very ancient domestication and use in Europe and other continents which in turn is probably the reason for the overlapping of characters among these species [45,54]. The frequent phenomena of natural [55,56] or artificial hybridization between some of these species is well known, even if only some hybrids between *P. salicina* or *P. cerasifera* and *P. armeniaca* or *P. mume*, known as plumcots, are of growing commercial interest together with other trademarked hybrids of the second generation, such as pluots, aprium, peacotum and nectaplum [4,57], often characterized in the new selections by high attractiveness (fruit size and color), taste and nutraceutical value. Hybridization is also commonly practiced for the rootstock breeding, aiming at tolerance to drought or resistance to disease.

The results of testing several interspecific cross combinations among a wide range of *Prunus* species showed different degrees of combining ability, measured as a percentage of the fruit set, indicating differently close taxonomic relationships. The highest compatibility was that of *P. cerasifera* with most of the other tested *Prunus* species and a much better fruit set was found when crossing *P. domestica* with *P. armeniaca* than with *P. salicina* [58]. Accessions of several plum related species have been suggested as potential donors of useful tree and fruit traits to be used in breeding programs [56]. A partial overview of some of this genetic potential for plum breeding is given in Table 1.

Table 1. A list of potential useful traits presented by different plum-related species.

Related Species	Positive Traits		Negative Traits	Ref.:
	Tree	Fruit		
<i>P. simonii</i>		flat fruit shape, small stone, flesh firmness, acidity, aroma		[55,56]
<i>P. cathayana</i>		sweetness		[56]
<i>P. limeixing</i>	late-flowering or frost-resistance	pubescent fruit surface, flesh firmness, aroma		[56]
<i>P. mume</i>	early blooming			[59]
<i>P. cerasifera</i>	cold hardiness good productivity, resistance to bacterial spot, drought and heat, early maturity, and tolerance to unfavorable conditions		medium to small fruit size	[35,60]
<i>P. spinosa</i>	drought resistance, cold hardiness dwarfing	blue fruit color		[60]
<i>P. microcarpa</i>	drought resistance; heat resistance			[60]
<i>P. americana</i>	cold hardiness; tough skin		suckering	[9,60]
<i>P. angustifolia</i>	low chilling requirement; resistance to bacterial spot		suckering, limited tolerance to plum leaf scald; small fruit size	[20,48,60]
<i>P. ussuriensis</i>	cold hardiness			[60]
<i>P. besseyi</i>	late bloom, frost resistance, resistance to crown gall		sensitivity to <i>Monilinia</i> spp.	[20,48,60]

Table 1. Cont.

Related Species	Positive Traits		Negative Traits	Ref.:
	Tree	Fruit		
<i>P. maritima</i>	frost resistance, late bloom, high heat requirement; salt tolerance			[48,60]
<i>P. alleghaniensis</i>	resistance to crown gall		small fruit size; bitterness	[20,48]
<i>P. geniculata</i>	drought tolerant, low chill		small fruit size	[20,48]
<i>P. hortulana</i>	resistance to bacterial spot	bright skin color	small fruit size	[20,48]
<i>P. munsoniana</i>	productive	good fruit quality		[20]
<i>P. subcordata</i>	drought tolerance		high chill requirement	[20,48]
<i>P. nigra</i>	cold hardiness			[20]
<i>P. umbellata</i>	resistance to crown gall		poor fruit quality	[20,28]
<i>P. texana</i>	precocity	fair quality		[4,48]

3. Plum Species Characteristics, Origin and Diversity

3.1. European Plum (*P. Domestica* L.)

There is a general consensus [19,50,61] that *P. domestica* is most likely an interspecific hybrid of *P. cerasifera* (2×) and *P. spinosa* (4×) that was introduced into Europe only after a long period of cultivation and human selection in the mountainous area of origin of the Caucasus, between the Black Sea and the Caspian Sea, where the alleged progenitors are also distributed. However, considering that *P. spinosa* itself is an inter-specific hybrid between the diploid *P. cerasifera* and a second, unknown *Prunus* ancestor, an origin of *P. domestica* from complex interspecific hybrids, and possible contributions from other Eurasian plums such as *P. ramburii*, cannot be excluded [19,62,63]. European plum cultivation has a long history in Europe, where it may have played a significant role in the development of early agrarian societies, and also had the advantage of being able to be preserved for a long time once dried. The first mention of European plums appears in the seventh century B.C. [3], followed in the Roman era by classic authors like Virgil, Cato, Ovid, Pliny, and Columella that unequivocally testify that the cultivation of the plum is in debt to the romanization of Europe [4,52,64].

The European plum, compared to the Japanese type, is generally adapted to temperate, cooler regions, and is characterized by a more upright tree growth habit, a more pronounced slowness to bear and the prevalent presence of mixed shoots. The European-type cultivars are mainly self-compatible, though cross pollination is always advantageous, as well as providing an adequate number of beehives in the orchard. However, an excessive crop load, not controlled by pruning or thinning, enhances the tendency to alternate bearing [65]. The chilling requirement is between 600 and 1300 chilling hours (C.H.) [66]. The flowering is not very scalar; the flowers have white petals and are commonly produced by isolated buds. Flowering usually occurs between early March in southern locations and mid-March in northern locations in California [65], and between late March and early April in continental Europe, while fruit ripening, depending on the cultivar, may extend from June to October but is more concentrated between July and August. European plums have an ovoid, ellipsoidal or flask fruit shape, as in the case of the oldest plums; more rarely they are globose. The fruit color ranges from black to blue, purple, red and yellow, while the flesh ranges from orange to yellow and greenish yellow to white [60]. They are generally freestone, or with only a small area of adhesion to the flesh, with peduncles that easily detach from both the fruit and the branch so that they can be easily harvested mechanically by shaking, unlike the Japanese ones which are harvested exclusively by hand.

European plums are usually more flavored and have a higher total content of soluble solids (SSC) than Japanese cultivars. They may be eaten fresh, canned, dried, or, especially

in the case of small unmarketable fruits, can be processed into juice or for confectionery uses, for jam making, spirit production (slivovitz, tuica, pálinka) and baking products [67]. European plum cultivars very popular in Middle and Eastern Europe, such as 'Italian Prune' and 'German Prune', that can be destined for all these uses, are considered as multipurpose cultivars [68].

The term "prune", generally applied to European plums, is more correctly appropriate to indicate a pomological group, having 'Stanley' as reference cultivar, in which the fruit is usually reddish or blue, elongated, with a high sugar content (up to 22–24° Brix), a fruit size between 30 and 40 g, and high flesh firmness, therefore with excellent drying characteristics [3,60]. However, some of the main cultivars, such as 'President', 'Stanley', 'Reine Claude', and others are considered suitable for both fresh and dry use (i.e., can be considered as dual-purpose cultivars). In other words, although all prunes are plums, not all plums can be dried into prunes, dealing with problems of fermentation at the pit. However, recently the use of the term "dried plum" instead of "prune" has been preferred [69]. Typical prunes are 'Prune d'Agen' and 'German Prune', which is the most spread prune in Europe, with many synonyms ('Commun Plum', 'Hauszwetsche' in Germany, 'Požegača' in Yugoslavia, 'Besztercei' in Hungary, 'Casalinga' in Italy, 'Quetsche Commune' in France, 'Vinete-romanesti' in Romania and 'Kustandilska' in Bulgaria) [58].

3.2. Japanese Plum (*Prunus Salicina* Lindl.)

Prunus salicina is reputed to have originated in China, in the Yangtze River basin, where it has been domesticated from ancient times and was introduced to Japan in the mid 700s [3]. This species, closely related to *P. armeniaca* [59] and to *P. mume*, a very early flowering *Prunus* species domesticated in China more than 3000 years ago as an ornamental plant and fruit [70], was initially improved in Japan but received special attention in the USA where it was imported in the last decades of the 19th century before it reached Europe [35].

The term Japanese plum, originally applied to *P. salicina*, now includes all the fresh-market plums developed by plant breeders to enhance fruit quality and plant adaptation by intercrossing different diploid species with the original species, so that this crop is considered a multispecies complex [28,71]. In fact, the modern cultivars of the Japanese-type are complex hybrids with Chinese (*P. salicina* and *P. simonii*), European (*P. cerasifera*), and American (*P. americana*, *P. angustifolia*, and *P. munsoniana*) pedigrees [70]. The analysis of genetic relationships among U.S. cultivated diploid plums and their progenitors ascertained that most of the genetic background to the modern-improved cultivars, as determined by RAPD markers, was from *P. salicina* (29% to 36%) followed by contributions from *P. simonii* (21% to 26%), *P. cerasifera* (21% to 28%) and *P. americana* (10%) [21]. According to Okie and Ramming [28], *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.

Cultivated Japanese-type plums are precocious bearers, have a generally expanded tree habit and are characterized by a chilling requirement between 120 and 780 chilling hours [66], which is lower than for the European ones, and heat requirements between 5300 and 10,000 GDH. This characteristic contributes to an earlier flowering with greater sensitivity to spring frosts. Most of the crop is borne on spurs. Self-incompatibility is predominant among cultivars and the blooming period is shorter amongst all stone fruits [72] and generally shorter than that of the European plum [60]. Japanese plum trees could have more than 100,000 flowers at full bloom, but insect attraction is poor [73], and the fruit set is generally very limited (5–14%), lower than other *Prunus* species [38]. Japanese plums are distinguished from the European ones for their attractive appearance and greater size (from 60–80 up to 150–160 g), the spherical-globose shape, the very pruinose skin, the colors very bright, usually monochromatic (light yellow, yellow amber, green-yellow or green-gray, pink-red, pink-purple, dark purple, blue, blue-violet) or mixed. Red or black skin color and yellow or red flesh color appear to be the most acceptable. Currently, the market is

dominated by black skin with light yellow or red flesh fruits [9]. They are not suitable for drying as they are too watery and have lower soluble solids contents (12–15% SSC on average) and are usually not even suitable for obtaining juices, only jams. Japanese-type plums generally have also lower acid contents and lower ratios of SSC to malic acid than European plums [74]. Fruit ripening varies greatly from June to October, depending on the cultivars. The high susceptibility to cold storage of some cultivars allows to extend the availability of the fruit by up to 60 days.

4. Plum Varietal Diversity

Within the large pomological groups of plums, a set of over 6000 cultivars of different species distributed in Asia, Europe and America has been estimated according to reports dating back to the beginning of the 20th century [4]. In the early 1980s, more than 2800 cultivars of plum of different types were utilized worldwide, according to Fogle [75] and Bellini [76]. However, currently very few of them maintain an economic significance for the plum industry worldwide.

On the other hand, these high, and perhaps overestimated numbers (due to duplications, synonymies, and cultivar disappearance over time) suggest in any case a great varietal diversity that is only partially known, exploited, and adequately preserved for present and future breeding opportunities [77].

To this end, numerous initiatives have been undertaken at the national and international level. In Europe, EUFRIN (European Fruit Research Institutes Network (<https://eufrin.eu>, accessed on 11 November 2021) and the European Cooperative Programme for Plant Genetic Resources (ECPGR; www.ecpgr.cgiar.org, accessed on 11 November 2021) coordinate the efforts to exchange scientific information, to ensure long-term conservation of this germplasm in Europe and to increase its utilization in breeding programs also by facilitating the access to the European Collections of selected accessions with valuable traits, under the rules of AEGIS (A European Genebank Integrated System; www.ecpgr.cgiar.org/aegis, accessed on 11 November 2021) [78]. A linked web-based catalogue that provides information about ex situ plant collections maintained in Europe is represented by EURISCO (<https://eurisco.ipk-gatersleben.de>, accessed on 11 November 2021). This database, under the guidance of ECPGR and Biodiversity International, is based on a European network of ex situ National Inventories (NIs) that makes the European plant genetic resources data available everywhere in the world [79].

The EURISCO Catalogue regarding plum (accessed on 11 November 2021) contains passport data about 5078 samples of *P. domestica* diversity (including subspecies *insititia*, *syriaca* and *italica*) from 25 different countries, and 261 accessions of *P. salicina* (including hybrids) from five countries (Figure 1). This represents a consistent increase (more than double) in comparison to the total number of accessions of plums and prunes recorded in 2007 [77], when 2254 accessions were included in the European Prunus database (EPD) and, successively, in 2011 when the number of plum accessions in EPD rose to 3300, second only to cherry accessions [80]. EPD was established in 1997 for the management of the Prunus genetic resource collections by the European Prunus Working Group which was created in 1983 under the auspices of IPGRI (now Biodiversity International), during the first phase of ECPGR [81].

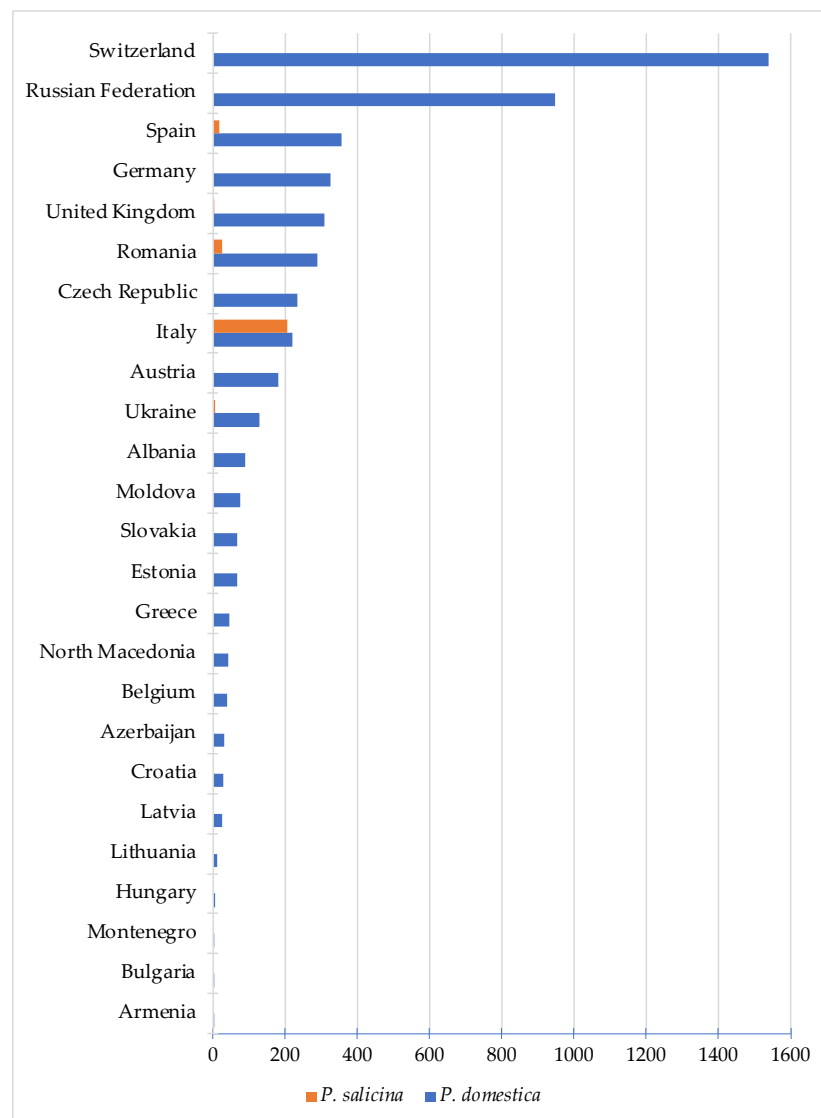


Figure 1. Number of accessions by country of European and Japanese plums, including subspecies and hybrids, cataloged by EURISCO (accessed on 11 November 2021).

The ECPGR Prunus Working Group was one of the first coordinated attempts to preserve European plum diversity, and is currently engaged in the same purpose. It extensively carried out coordinated activities funded by Bioversity International aimed at selecting the appropriate set of descriptors and molecular markers for *P. domestica* accessions to be used for genotyping and phenotyping the collected accessions. Detailed and comprehensive reports of the European *Prunus* Working Group activities are available from many authors [80,82–85].

Within these projects, morphological and genetic data were collected and analyzed on 104 accessions of local plums, conserved in 14 different European countries [49,86], and further extended to 165 accessions [87].

Very recently a new specific project for the “Improvement of Fruit Tree Data Inclusion” in the EURISCO database (acr.: FRUITTREEDATA), involving 11 European countries with the main objectives to increase the phenotypic information and update the listing of available material within EURISCO, was funded by ECPGR (ECPGR Fifth Call–Phase X-2019–2023).

Genetic and morphological studies of several local plum germplasm have been carried out for numerous European countries such as Norway and Sweden [88], Spain [89], Slovenia [90]; Croatia [64]; Serbia, Bosnia and Herzegovina, Macedonia and Montenegro [91];

Bulgaria [92,93]; Hungary [94]; Romania [95,96]; Italy [15,76,97–100] or for accessions of mixed provenance [19,49,101–103], also including, inter alia, Denmark, Estonia, Latvia, Belgium, Great Britain, Germany, the Czech Republic, Greece and Slovakia.

These studies, aimed at validating the pomological/taxonomic classification in use within the heterogeneous European plums and assessing their genetic diversity, represent a valuable contribution to the conservation, knowledge, and use of the plum germplasm for breeding purposes, thus possibly closing the existing gap of reliable morphological and molecular data [57].

In the USA, plant genetic resource (PGR) conservation is ensured by the USDA-ARS National Plant Germplasm System (NPGS). The NPGS is a genebank system whereby PGR collections are maintained at 19 locations throughout the United States. The dedicated GRIN-Global system provides a public interface facilitating genebank workflows, and access to germplasm and associated information (www.ars-grin.gov, accessed on 11 November 2021). The collected accessions include improved cultivars, breeding lines, landraces, and crop wild relatives (CWR), along with passport and trait evaluation data [104]. The total number of plums and plum-related species accessions held in the National Clonal Germplasm Repository (Davis, CA) is given in Table 2.

Table 2. Number of accessions held in the NCGR in Davis, California, per plum and plum-related species.

Group and Species	1989	1999	2009	2017	2017/1989 %
European:					
<i>P. domestica</i> (European plum)	0	141	154	193	
<i>P. bokhariensis</i>	3	3	2	2	
<i>P. spinosa</i>	21	5	8	23	
<i>P. cerasifera</i>	14	32	45	66	
<i>P. cerasifera</i> var. <i>divaricata</i>				27	
<i>P. insititia</i>	0	1	3	0	
Subtotal	38	182	212	311	818
Asian:					
<i>P. salicina</i> (Japanese plum)	92	40	63	77	
<i>P. salicina</i> var. <i>mandshurica</i>				1	
<i>P. salicina</i> var. <i>salicina</i>				3	
<i>P. simonii</i> *	2	3	3	8	
<i>P. hybrid</i> (plumcot, aprium, pluot, etc.)		59		130	
Subtotal	94	102	66	219	233
New World Plums:					
<i>P. americana</i>	1	4		11	
<i>P. rivularis</i>	0	0	0	3	
<i>P. hortulana</i> *	3	0	1	6	
<i>P. mexicana</i>	15	2	2	3	
<i>P. maritima</i> *	50	2	21	3	
<i>P. geniculata</i> *	0	0	0	1	
<i>P. alleghaniensis</i> *	0	3	2	0	
<i>P. angustifolia</i>	2	15	4	20	

Table 2. Cont.

Group and Species	1989	1999	2009	2017	2017/1989
<i>P. gracilis</i>	0	0	0	0	
<i>P. munsoniana</i> *	0	1	2	0	
<i>P. nigra</i>	0	1	0	1	
<i>P. umbellata</i>	0	0	0	7	
Subtotal	71	28	32	55	77
Other:					
<i>P. subcordata</i>	26	12	7	12	
<i>P. texana</i>	0	0	0	2	
<i>P. bifrons</i>	0	0	0	4	
<i>P. pumila</i>	1	0	1	0	
<i>P. pumila</i> var. <i>besseyi</i>	5	1	0	4	
<i>P. microcarpa</i>	0	0	0	3	
<i>P. tomentosa</i>	55	6	9	11	
<i>P. andersonii</i>	0	3	0	4	
<i>P. fremontii</i>	1	2	0	2	
<i>P. × cistena</i> (<i>P. cerasifera</i> × <i>P. pumila</i>)	1	0	0	1	
Subtotal	89	24	17	43	48
Total	292	336	327	628	215

Source: Prunus Crop Germplasm—Committee Prunus Vulnerability Statement—March 2017 (modified). * Indicates species with minimal representation that received higher priority for collection, due to the endangered conservation status in the wild and desirable traits expected to be provided by each of them.

Reported data suggest that, even if the total number has grown in the last two decades, at least for the accessions of the European and Japanese plums and new hybrids, a dramatic downward trend generally concerned almost all plum-related species, including native American ones. In the USA, according to Okie [48], who quote Wight [105], at the beginning of the 20th century, a set of more than 600 named plum cultivars, derived solely from American species (*P. americana*, *P. hortulana*, *P. angustifolia*, *P. munsoniana*, or combinations thereof), was cultivated. However, very few of these native cultivars are still available in collections [20,35].

The aforementioned data concerning the most commercially relevant species are also worthy of attention. A considerable part of these (one third) is today represented by new, very attractive, interspecific hybrids (plumcot, aprium, pluot, peachcot, plum cherry) of growing commercial interest [57]. The number of European plum accessions is more than double that of Japanese plums, and a vast majority of them (\approx two-thirds) are of domestic (USA) origin. Additionally, most of the collected accessions of Japanese plum in the GRIN-Global database are classified as “not available” or “historic”, which means that data exists in the database, but the genebank no longer maintains a living germplasm. As a whole, these data suggest a limited representation of existing diversity, especially for Asian-related species and Japanese plums, that deserves additional effort for collecting and establishing the germplasm at the repository, available to enhancement programs [20]. This is especially true if we consider that, according to Blažek [77], a large part of these genetic resources are being preserved in Russia, China, Japan and Iran, and also that a large, not deeply explored germplasm is represented by the related species (and by extant derived cultivars) that can provide an ‘untapped source of genetic material’ [35] in hybridization programs, both for cultivars and rootstocks.

In this context, Japanese-type plums can be considered, therefore, a good example of a narrow genetic base. This largely depends on the fact that the number of founding

clones in the developing California Asian-type plum industry was initially limited to just five parents, all released by the famous plant breeder and horticulturist Luther Burbank (1849–1926) in the late 19th and early 20th centuries: ‘Santa Rosa’, ‘Eldorado’, ‘Gaviota’, ‘Formosa’ and ‘Burbank’ [71,106]. Moreover, when breeding programs combined just a few founding clones with high selection pressure for a single trait of interest, as for example for adaptation to low chill areas, this resulted in an even narrower genetic background, as in the case of Florida plum germplasm.

For diploid plums and related progenitor species, results from RAPDs analysis carried out by [21] showed that *Prunus salicina* and *P. simonii* (both of Chinese origin) and *P. cerasifera* (from Europe) contributed the bulk (72% to 90%) of the genetic background to the cultivated diploid plum. In the same research, most of the commercial cultivated Japanese-type plums of the California gene pool were more similar to *P. salicina* than to other species and closely clustered together, with the exception of genotypes from the Florida breeding program, which included signs of introgression of a Taiwan low chill plum genotype [107]. Clearly apart resulted also hybrids such as ‘Methley’ and ‘Wilson’, (*P. salicina* × *P. cerasifera* and vice-versa, respectively), and ‘Bruce’, ‘Segundo’, and ‘Robusto’ (*P. angustifolia* hybrids).

With regard to European plums, Horvath and colleagues [50], studying the chloroplast DNA genetic diversity in plum species (*P. domestica*, *P. spinosa*, *P. cerasifera*) in a French germplasm collection, found that the last two species had five to seven times more allelic richness than *P. domestica*, respectively. They also reported that most of the European plum haplotypes belonged to only two haplotypes, representing 80% and 16% of the 80 varieties studied, respectively. Overall, these data led the authors to conclude that when plums were first introduced in Western Europe, this introduction was by a limited number of founders, similar to what happened for the Japanese plum, albeit at different, more ancient times. Another study conducted on genetic diversity and structure of Spanish *Prunus domestica* germplasms has also reached similar conclusions [89].

5. New Plum Cultivars Obtained by Breeding

In the period 1980–2008, a total of 509 and 273 new plum cultivars of the Japanese and European type, respectively, were released worldwide [108]. This means that breeders have been releasing about 30 plum cultivars every year in the considered period.

A detailed overview of new plum cultivars obtained by breeding worldwide is offered by the registers of new fruit and nut cultivars, published by the American Pomological Society.

Examining these registers for the period 2000–2020, it emerged that in the USA a total of 198 new varieties of different plum types were registered in the first twenty years of the new millennium, most of them (46%) of hybrid origin (plumcots), followed by Japanese-type plums (43%), while only 11% were European plums (Table 3). Most of them were mid or mid late-season plums (47%), followed by early or very early-ripening (32%) and late-ripening plums (21%). As a whole, the most numerous group (48 new cultivars) was that of mid-season hybrids, followed by early or very early-ripening Japanese plums (38 cultivars). As far as the country origin of these new cultivars is concerned (Table 4), 91.5% of them were obtained in the USA, mainly in California (85%), and the remaining 17 cultivars, of which eight European plums, seven Japanese plums, and two hybrids, were from Canada (six cultivars); Italy (four); Australia (two); South Korea (two); Chile (one); Israel (one) and South Africa (one). Private breeding contributed most of the new cultivars (88.4%), whereas public breeding showed a downward trend over the years, consistently with what has been reported by several studies about declining plant breeding capacity in U.S. institutions [109,110].

Table 3. Number of new registered varieties in the USA, per plum type and year (2000–2020), according to ripening period.

Yr.	EP ^z			JP ^z			Hybr.			TOT.			Total
	E ^y	M ^y	L ^y	E ^y	M ^y	L ^y	E ^y	M ^y	L ^y	E ^y	M ^y	L ^y	
2000				2						2	0	0	2
2002		3		2	2		3	5	1	5	10	1	16
2004	1	1	1	11	3	2	7	1	2	19	5	5	29
2006	1	1	1	9	7	4	4	2		14	10	5	29
2008	1	2	1	2	2	1	1	3	2	4	7	4	15
2010				3	3	3	2	17	7	5	20	10	35
2012				1	2	3	2	3	2	3	5	5	13
2014				1				13	8	1	13	8	22
2016		7	1	1	2		1	2	1	2	11	2	15
2018				3	7	3				3	7	3	13
2020				3	3	1		2		3	5	1	9
Total	3	14	4	38	31	17	20	48	23	61	93	44	198

^zEP = European Plums; JP = Japanese Plums—^yEarly; ^yMedium; ^yLate. Source: Processed data from U.S. Register of New Fruit and Nut Varieties—List 40–50, HortSci. (2000–2020).

Table 4. Consistency of new registered varieties in the USA, per year (2000–2020) and origin (public or private breeder, inside/outside USA).

Year	Pub.	Priv.	Pub.	Priv.	USA	Other Count.
	N ^o		%			
2000	2		100	0	2	0
2002	5	11	31.3	68.7	15	1
2004	4	25	13.8	86.2	29	0
2006	2	27	6.9	93.1	29	0
2008	6	9	40.0	60.0	9	6
2010	1	34	2.9	97.1	32	3
2012		13	0.0	100.0	13	0
2014		22	0.0	100.0	22	0
2016	3	12	20.0	80.0	9	6
2018		13	0.0	100.0	13	0
2020		9	0.0	100.0	8	1
Total	23	175	11.6	88.4	181	17

Source: Processed data from U.S. Register of New Fruit and Nut Varieties—List 40–50, HortSci. (2000–2020).

On average, the least represented class size was that of new cultivars with very small fruit (1.6%), and the most was that of “large” (36.8%). Within each plum type, “large” was the prevailing fruit size for both Japanese and European plums (40.7 and 33.3%, respectively), whereas “medium” prevailed for interspecific hybrids (38.5%) (Figure 2). It should be noted, however, that the standard for dried prunes ranges from small to medium size fresh fruit and is, therefore, different from that of Japanese and interspecific plums. Concerning the origin of the new cultivars, controlled cross among selected genotypes was the prevailing breeding applied method for both European plums and hybrids, while open pollination was the primary method for Japanese plums (data not shown).

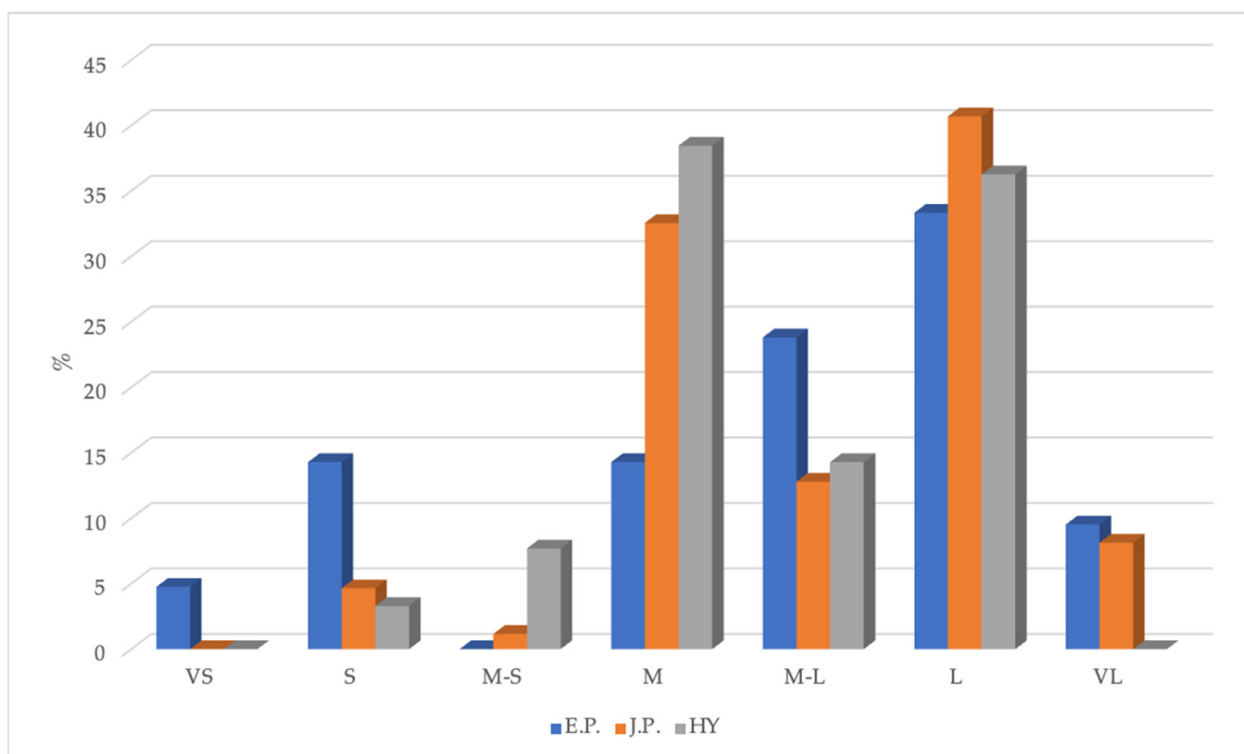


Figure 2. Fruit size distribution of new released cultivars in the U.S. Register of New Fruit and Nut Varieties (2000–2020) for European plum (E.P.), Japanese plum (J.P.), and interspecific hybrids (HY). Fruit size are as follows: VS = very small; S = small; M-S = medium to small; M = medium; M-L = medium to large; L = large; VL = very large.

Eleven out of 21 European new plum cultivars were self-compatible (52%), as well as eight out of 86 Japanese plums (9%) and only one out of 91 (1.1%) interspecific hybrids. More than 60%, about 30% and 12% of European, Japanese and hybrid new cultivars, respectively, were free- or semi-freestone. In the majority (66%) of all the new released cultivars, the growth habit was semi-upright or upright, followed by spreading or semi-spreading habit (23%) and by upright to spreading (11%), and this ranking was true also within each plum type. Data regarding chill requirements were not available for all of the cultivars. However, high chill (> 600 C.H.) was prevailing both for Japanese plums and interspecific hybrid cultivars, followed by intermediate (>400 ≤ 600 C.H.) and by very few (6) low-chill (<400 C.H.) Japanese plum cultivars, namely ‘Gulfbeauty’, ‘Gulfblaze’, ‘Gulfrose’, ‘Yellow #503’, ‘Suplumtwentyfive’ and ‘Suplumthirtyeight’. On the contrary, the ‘Bella Zee’ interspecific plum had the highest chill requirement (1000 C.H.). Table 5 reports the list of plum cultivars with reported disease resistance or tolerance registered in the last twenty years. Very few cultivars presented resistance/tolerance to bacterial spot (6); to leaf scald (4), bacterial canker (9), black knot (7) and only one to PPV, ‘Honey Sweet’, which represents the first genetically engineered plum pox virus-resistant European plum cultivar [111].

The Fruit Research Institute of Čačak (Serbia) has recently presented the objectives of its genetic improvement program (fruit quality, high and regular productivity, early and late harvest time, tolerance, or resistance to Sharka (PVV), and adaptability to different climatic conditions). From this program, nine new PPV-tolerant cultivars were released in the last 15 years: ‘Boranka’ (‘California Blue’ × ‘Ruth Gerstetter’), ripening in early July, suitable for fresh consumption; ‘Timočanka’ (‘Stanley × California Blue’), ripening in the first ten days of August, suitable for the fresh market; ‘Mildora’ (‘Large Sugar Prune’ × ‘Čačanska Lepotica’), ripening in the last ten days of August, small fruit (20–30 g), reddish, of very high quality (25–30 °Brix), of particular interest for drying; ‘Krina’ (‘Wanghenheims

Frühzwetsche' × 'Italian Prune'), ripens in late August-early September, suitable for fresh consumption and processing; 'Zlatka' ('Large Sugar Prune' × 'Žolta Butilkovidna'), ripens in the last ten days of August, suitable for processing; 'Divna' ('Stanley' × 'Čačanska Rana'), ripening in the first half of September, medium-large deep blue fruit (30–35 g) with yellow-green flesh, both for fresh and processed consumption; 'Petra' ('Stanley' × 'Opal'), ripening in the first half of September, medium-large deep blue fruit (30–35 g) with yellow flesh, intended both for fresh and processed consumption; 'Pozna Plava' ('Čačanska Najbolja' × 'Čačanska Najbolja'), ripening in the first ten days of September, of excellent quality, suitable for desserts and processing; 'Nada' ('Stanley' × 'Scoltus'), ripens in mid-August, suitable for desserts and processing, together with many promising hybrids [32]. Lastly, 'Lana' was developed for fresh consumption by the planned hybridization of 'California Blue' × 'Ruth Gershtetter'. This cultivar is characterized by early ripening (four to ten days after 'Čačanska Rana') and tolerance to PPV. The fruit is large, the skin is purple blue, and the flesh is yellow-greenish, moderately firm, juicy and aromatic, with a sweet-subacid flavor [112].

Table 5. List of plum cultivars in the U.S. Register of New Fruit and Nut Varieties (2000–2020) with reported disease resistance (R) or tolerance (T).

Cultivar	Plum Type ^(z)	Bacterial Spot	Bacterial Canker	Leaf Scald	Black Knot	PPV
Spring Satin	Hy	R	R	T		
Gulfbeauty	JP	T		R		
Gulfblaze	JP	T		R		
Gulfrose	JP	T		R		
Mann	JP		R			
Queen Garnet	JP	R				
Ruby Queen	JP	R	R			
Vampire	JP		T		T	
Honey Sweet	EP				R	R
Valerie	EP		R		R	
Vandor	EP		R		R	
Vanette	EP		R		R	
Vibrant	EP		R		R	
Violette	EP		R		R	

^(z) European plum (EP), Japanese plum (JP), and interspecific hybrids (Hy).

In California, six advanced selections, which are currently under consideration for release to the California dried fruit industry, have been presented recently [37]. These selections are characterized by superior dried fruit flavor; exceptional fruit firmness and adaptability to mechanical harvesting, commercial dehydrating, mechanical sizing, pitting and packaging.

In Italy, Bologna University's plum breeding program released the European cultivars 'Sugar Top' and 'Prugna 29', and the Japanese cultivars 'Black Glow' and 'Black Sunrise'. Together with a private-industry partner consortium, they have so far identified 30 Japanese and 10 European selections. 'Black Glamour' ('Black Amber' × 'Howard Sun') is a new early bearing, high-quality, black skin, yellow-flesh Japanese plum characterized by large fruit size, pronounced firmness and juiciness, good flavour, suitable for flexible picking (maintains ripeness on tree for nearly a month), and with good postharvest storability [113]. In Spain a breeding program carried out in the southeast region of Murcia [114] presented several advanced selections and two new early ripening, high quality Japanese plum cultivars ('Lucia Myrtea' and 'Victoria Myrtea'), characterized by red flesh, very low chilling

requirements and good adaptation to warm areas. In Germany, as well, a wide activity of genetic improvement has been carried out for European plums and many new cultivars have been released (e.g., ‘Emma’, ‘Miroma’ and ‘Fidelia’) in the last 15 years [68]. Some of them are also considered useful donors for specific traits in many breeding programs (Table 6).

Despite the large availability of newly released cultivars including several dozen other cultivars that have been released elsewhere in the last 30 years [68,96,115–123], the variety assortment that constitutes the bulk of the plum tree industry in the various main producing countries continues to be dominated by a small number of well-established varieties, with the few exceptions mainly constituted by new interspecific hybrids such as, for example, those of the Metis group [124]. In Spain the market offer is currently dominated by about six to seven cultivars, including ‘Angeleno’, ‘Black Splendor’, ‘Crimson Glo’ and ‘Golden Glo’; in Germany by ‘Top’, ‘Hanita’ and ‘Cacaks Schöne’; in the eastern European countries by ‘Stanley’, ‘Čačanska Lepotica’, ‘Čačanska Rodna’, ‘Anna Späth’, ‘Tuleu Gras’, ‘Vinete Romanesti’, and ‘Grase Romanesti’.

In Italy, in the early 1980s, a total of 44 Japanese plums were reported by Bellini (1980) for being of some interest for the Italian plum industry. At that time, they covered a harvesting season of 80 days starting from June 26 (‘Ruth Gerstetter’) to September 13 (‘Burton’), and 68 days, from 20 June (‘Red Beaut’) to 26 August (‘Casselmann’) for the European and the Japanese plums, respectively. About twenty years later, only 21 Japanese and seven European cultivars of plums were included in the list of suggested cultivars for Italy [125] but with an extended harvest period (20 June–20 September and 25 June–25 September). In a further subsequent list for Italy, Liverani et al. [126] reported a total of 18 Japanese and five European cultivars as of general interest for the Italian plum industry overall, covering a similar harvesting season to what previously reported. Unfortunately, this national public program of plum cultivars evaluation was thereafter discontinued, and thus generalized evaluation is no longer available. However, from this program the emerged negative evaluation affecting several European and Japanese cultivars, maintain its validity. This is the case for Italy of ‘Empress’, ‘Excalibur’, ‘Felsina’, ‘Firenze 90’, ‘Maria Novella’, ‘Presenta’, ‘Sugar’, ‘Sugar Top’, ‘Tegera’, ‘Tipala’, ‘Top P3’, ‘Topfive’, ‘Tophit’, ‘Topking’ and ‘Topper’, and the Japanese cultivars ‘Beauty Sun’, ‘Black Gold’, ‘Black Star’, ‘Globe Sun’, ‘Larry Ann’, ‘Obilnaja’, ‘October Sun’, ‘Ozark Premier’, ‘Royal Diamond’, ‘Susy’, ‘Tardiva di Scanzano’ and ‘Tracy Sun’ that were not further recommended, mainly due to poor and inconsistent productivity and susceptibility to *Xanthomonas* spp. and leptonecrosis. Currently, among the most cultivated varieties are the Californian ‘Angeleno’, ‘TC Sun’, ‘Black Diamond’, ‘Fortune’ and the early Italian ‘DOFI-Sandra’. The most widely grown European cultivars are ‘Ente 707’ for drying, ‘President’ for fresh consumption and ‘Stanley’ for both uses [127].

On the other hand, in the last years the most appreciated cultivars in the Italian market have been, until mid-July, ‘Anna’, ‘Aphrodite’, ‘Black Splendor’, ‘Santa Rosa’, ‘Crimson Glo’ and ‘Golden Plum’; afterward, until the end of August, ‘TC Sun’ and, among the European plums, ‘Stanley’, ‘Regina Claudia’, ‘Grossa di Felisio’ and ‘President’ and, lastly, the late ripening ‘Fortune’, ‘Angeleno’, and ‘Autumn Giant’.

6. Modern Breeding Objectives and Programs

The evolution of consumer preferences and expectations, together with the need to face the new challenges imposed by marketing competition and technological, agronomic, and environmental problems, including climate change and ecological sustainability, continually push research towards the enhancement of the plum variety assortment via the obtainment of new valuable, superior cultivars.

Plum and prune breeding programs have been traditionally focused on common objectives regarding both the tree and the fruit characteristics. Not differently from other stone fruits, e.g., peach, widening ripening time and fruit availability on the market, improving fruit quality and appearance and the search for resistance or tolerance traits

to abiotic and biotic stresses, have been all characters of paramount interest for breeders. For the fresh stone fruit market Byrne [109] enumerates, inter alia, diversification of fruit types; increased interest in the health benefits of fruit; increased demand for fruit quality and need for better postharvest traits, as the main drivers of modern breeding programs. Specific objectives for plum include late blooming, self-compatibility, short growing period, spur fructification, regular productivity, and frost resistance [57].

For Japanese plum, large fruit size, enhanced firmness for postharvest sorting, storage, and transport, upgraded flavor and taste properties like texture, juiciness, and sweet/sour balance, and distinctive red flesh coloring in response to consumer preferences have been targeted by breeding programs worldwide [113,128]. Concerning tree aspects of main interest for growers, climatic adaptability, productivity, resistance, especially to PPV, are commonly desired traits. On the other hand, more recently, tree architecture, growing habit and vigor, and adaptation to mechanical harvesting, have been included in Californian breeding programs for European drying prunes [37] to limit both growing and drying costs. In the low-chill regions much of the breeding efforts focuses on intercrosses plums presenting resistance to bacterial leaf spot, plum leaf scald, bacterial canker, and rust, and having low-chilling requirements with others having better fruit quality [129]. Furthermore, these goals have become of generalized relevance in the current context of global warming [114].

The most applied breeding techniques are traditional horticultural breeding practices such as controlled cross among selected genotypes and clonal selection of autochthonous cultivars with the aim of combining, to the best possible degree, as much of the best selected parents' horticultural traits and a minimum of their negative characteristics. For this reason, the knowledge of the parents' breeding history and pedigree is of fundamental importance [37]. Nevertheless, genetic gain in the progenies and therefore good results of breeding programs cannot be taken for granted, mainly due to the different nature and heritability of the numerous genetic traits involved [130]. Even well-known and established cultivars such as the "Improved French" prune in the U.S. proved to not be a good choice as a parent, due to the long juvenile time period and the low heritability of the high fruit yield trait [69].

Good progress for several traits when compared to the selected parents used for hybridization has been reported by Botu and Botu [131]. Encouraging results in Romania as a result of using selected parentages with very well-known characteristics and pedigrees have been obtained for fruit size, ripening time, productivity, and tolerance to PPV with respect to the utilized parents [96]. Priority source genotypes for breeding purposes have been identified within the Russian plum collection maintained at the North Caucasus Federal Scientific Center of Horticulture, Viticulture, Winemaking (Krasnodar, Russia) and reported by Zaremuk et al. [132].

However, since the conventional breeding processes are inevitably time consuming and costly, special expectations rely on innovative biotechnological approaches and on improved knowledge of the inheritance of specific traits to develop suitable molecular markers for marker-assisted selection (MAS) and thus fostering the efficiency of breeding programs [133].

The following is a non-exhaustive list of traits of interest for breeding with potential donors (Table 6).

The main and most recent goals and results of plum tree breeding, together with its history, have been listed by UPOV [134], and reviewed and summarized by the USDA, [136] Okie and Ramming [28], Hartmann and Neumuller [60], Neumuller [58], Topp et al. [4] and very recently by Milošević and Milošević [57] and by Neumuller et al. [135] who reports, together with the new released cultivars 'Franzi' and 'Moni', a series of new challenges for cultivar breeding.

Table 6. List of traits of interest for plum breeding cultivars and potential donor genotypes, according to different sources.

Problem/Researched Trait	Potential Donors with Improved/High Trait		References
	European Plums	Japanese Plums	
Primary/Traditional			
Early blooming	'J2N-127', 'Graf Bruhl', 'Lutzelsachser Fruhwetsche'		[37,134]
Late Blooming	'Blue Bell', 'Italian Prune', 'Pitesteau'		[60,134]
Low chilling requirement		'Gulfblaze', 'Gulfbeauty', 'Victoria Myrtea'	[107,114]
Early maturing	'J15S-22', 'J16N-95', 'Ruth Gerstetter'	'Spring Satin', 'Lucia Myrtea', 'Victoria Myrtea'	[35,37,114,129]
Late maturing	'Elena', 'Reine Claude de Bavay', 'Presenta'	'Fallette', 'Holiday', 'Ruby Queen'	[35,60,134]
Climatic adaptation	'Prune d'Agen', 'Italian Prune', 'Stanley', 'German Prune'		[58]
Fruit size	'J17S-30', 'President', 'Jubileum', 'Tophit', 'Haganta', 'Lana', 'Pagane', 'Grossa di Felisio', 'Kabardinskaya Rannyaya'	'Plumcandy XIV', 'Suplum Fiftyfour'	[37,60,111,122,124,128]
Self-compatibility	'Muir Beauty', 'Stanley', 'Anna Späth', 'Bluefre', 'Ialomiza', 'Diana', 'Andreea'	'Victoria Myrtea'	[69,96,114,135]
Productivity	'Muir Beauty', 'Grase de Pesteană', 'Stanley', 'Anna Späth', 'Bluefre', 'Standard', 'Grase de Becs', 'Čačanska Lepotica'		[95,96]
Fruit taste and quality	'Nada', 'Mildora', 'Kabardinskaya Rannyaya', 'Oneida', 'Andreea', 'Grase de Becs'	'Hanita'	[60,96,123,128]
High sugar content	'F11S-38', 'J4N-119', 'Sugar Top', 'Mildora'		[37,123,124]
High flesh firmness	'Hauszwetsche', Nordens, 'Katinka', 'Tegera', 'Čačanska Lepotica'		[60,134]
Floral precocity	'H13S-58', 'I12S-6', 'Stanley', 'Čačanska Lepotica', 'Čačanska Rodna', 'Verity'		[37,60]
Resistance to PPV	'Moni', 'HoneySweet', 'Jojo', 'Boranka', 'Timočanka', 'Mildora', 'Krina', 'Zlatk'a, 'Pozna', 'Plava', 'Nada', 'Jofela', 'Jolinda', 'Jocanta', 'Divna', 'Petra', 'Lana', 'Grase de Becs', 'Uriase de Sibiu'		[58,69,95,96,111,120,121,123,135]
Resistance to leaf scald		'SC7'	[119]
New/Additional			
Low fresh to dry fruit weight loss	'HoneySweet', 'F11S-38', 'F11S-38'		[37,111]
Storage ability		'Vampire'	[136]
Abnormal June fruit drop	'Katinka', 'Juna', 'Moni', 'Haroma'		[135]
Frost tolerance	'Franzi', 'Hauszwetsche', 'Mirabelle de Nancy', 'Schönberger', 'Italian Prune', 'German Prune'		[60,135]

Table 6. Cont.

Problem/Researched Trait	Potential Donors with Improved/High Trait		References
	European Plums	Japanese Plums	
Primary/Traditional			
Winter hardiness	'Vengerka Moskovskaya', 'Zuysinskaya', 'Reine Claude Reform'		[58,135]
Heat susceptibility (damage in the flesh)	'Moni'		[60,131]
Stone cracking			[135]
Twin fruits	'Hauszwetsche', 'Katinka', 'Juna', 'Čačanska Rodna'		[58,60,135]
Orange flesh color		'Hanita', Gulflaze, 'John W.', 'Sugar Top'	[58,136]
Red flesh color		'Lucia Myrtea', 'Victoria Myrtea', 'Vampire', 'Plumred X, Plumsweet (series)', 'Suplumfortyseven to Suplumfiftyone (series)'	[114,136]
Caverns and pectin inclusions	'Moni'		[135]
Freestone pit	'Hauszwetsche', 'Kirke's', 'Čačanska Lepotica', 'Tegera', 'Katinka', 'Sutter'		[60,69,134]
Processing suitability ^(z)			[69]
Good tree structure ^(z)			[37]
Uniformity in fruit maturation ^(z)			[37]
Slow fruit softening near harvest time ^(z)			[37]
Plum decline: <i>Pseudomonas syringae</i> resistance ^(z)			[135]
<i>Drosophila suzukii</i> resistance ^(z)			[135]

^(z)Desired trait, not yet well documented/or depending on more than one single trait.

7. Conclusions

Since its inception, plum cultivation has benefited enormously from the strong impetus provided by genetic improvement. The high variety of forms, fruit size, color, texture, shape and taste, and degree of adaptation to cultural environments existing within plum groups and among plum cultivars is outstanding in the context of modern fruit culture worldwide. This varied diversity, together with the broader germplasm resources made up of what can collectively be defined as its agrobiodiversity (old traditional cultivars, landraces, related species, or wild progenitors), represents a rich reservoir of genetic traits within which it is still largely possible to draw important sources of traits, especially of genetic resistance, useful for the further genetic improvement of the crop. In other words, and also in the case of plums, it is possible to affirmatively answer the question posed by Koebner and Ortiz [137]: Fishing in the gene pool—how useful was the catch? In fact, although several factors such as proper site selection, crop load, harvest time, phytosanitary status, cultivation techniques, rootstock and so on, can significantly affect fruit productivity in plums, the genotype remains the key factor for further enhancing fruit

quality. Breeding efforts to develop superior new cultivars that meet the demands of new production systems, ecological sustainability, and human health, and coordinated efforts for plum germplasm conservation are the challenges to be addressed to further improve the plum industry worldwide.

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