

Alireza Rahemi
Thomas M. Gradziel

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Identification, Characteristics and Uses

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Foreword

Since ancient times, almond kernels have been considered a desirable and healthy food. Almonds are both whole and processed, giving rise to a large number of derived products not only for direct human consumption but also the use of its oil for cooking as well as the pharmaceutical and cosmetic industries. References to almond cultivation and use date back to the Old Testament of the Bible and Greek mythology.

The almond tree is native to Central Asia, although a few wild almond trees can also be found in the Middle East as possible ancestors of the current cultivated almond tree. These include *Prunus webbii* and *Prunus orientalis*. Wild stands of these and related almond species can still be found in many countries in those areas. In Central Asia, there can also be found cultivated forms of almond derived from successive crosses with these wild species. Similar gene Introgression has occurred in the Mediterranean area with the naturally occurring wild species, including *P. webbii*.

In its westward expansion, almond cultivation was introduced to countries surrounding the Mediterranean Sea, where suitable environmental conditions were present. Desirable conditions include mild winters with hot, dry summers, typical of Mediterranean climates. Cultivated almond shows a high tolerance to summer drought and heat. Over the ensuing centuries of production, successive improved selections made by man have given rise to a range of varieties better adapted to regional soil conditions and climate as well as consumer preferences.

Recent changes in climate conditions and cultivation techniques are currently testing the versatility of the almond tree to adapt to the realities of the twenty-first century. Resources available to meet these challenges include a wide diversity of cultivated germplasm, as well as an even greater genetic diversity in the wild species available for breeding improved rootstocks and varieties.

By observing the vegetative characteristics of the plants in their places of origin, it can be deduced that some of these species could contribute characteristics of value to crop improvement.

Collections of cultivated varieties and also of some of the wild species, including some interspecies hybrids, have been gathered in several research centers in order to try to incorporate some of the favorable characteristics present in them into the breeding material. An example would be the incorporation of self-fertility to the species in culture from the close presence of *P. webbii*.

For variety improvement, the use of wild species is particularly challenging in the short and medium term, because of the distance between their characteristics and current market demands.

For rootstocks, the situation can be considered more favorable. Wild species and their hybrids demonstrate adaptation to poor soil conditions, including their possible improved uptake efficiencies for both water and nutrients. Further evaluation will be required to assess their ultimate effect on rootstock performance (size, productivity, and branching habits) of grafted variety under commercial orchard conditions.

This work (book) includes in its chapters knowledge and techniques for the possible use of the interesting characteristics of wild almond species to improve almond cultivation through their genetic incorporation for variety and rootstock improvement. Topics include:

- An introduction to almond species and their origins
- Almond species classification
- Characteristics of almond species
- Identification of almond species by using markers
- Self-incompatibility in almond species
- Seed germination of almond species
- Almond species traditional utilization
- Utilizing related species for cultivar and rootstock improvement

This contribution to the knowledge on almond tree species—wild and cultivated—provides one more step for the continued improvement of almond varieties and rootstocks are now.

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Antonio J. Felipe

Preface

Almond species represent one of the most successful ecological as well as horticultural groups in the genus *Prunus*, Family Rosaceae. Classified to the subgenus *Amygdalus*, species occupy important positions in ecological habitats ranging from the Mediterranean in the East to the Yangtze River in the West and include the commercially important tree crops: almond, peach, nectarine as well as important rootstocks for almond, peach, nectarine, plums, prunes, and apricots. While human selection for fruit and nut quality has resulted in severe inbreeding in commercial varieties, natural selection has evolved an enormous diversity as a readily intercrosses ball court genome diversified during adaptation to climates ranging from high altitude xerophytic habitats in central Asia to the subtropical conditions of southern China. While climate change threatens both wild and cultivated species, the accumulated genetic diversity combined with the absence of serious barriers to interspecies gene transfer offers opportunities for the survival of both groups. For this to happen, a fuller characterization of this germplasm is required, particularly for those accessions adapted to the extremes and, thus, most vulnerable ecosystems.

In recent years, almonds have become a major nut crop in world production. Because much of this production is based on a very narrow genetic base, crop improvement programs are scrambling to identify and incorporate useful wild germplasm to improve productivity as well as disease, pest, and environmental stress resistance. This germplasm also provides the opportunity to dramatically alter the traditional crop, as occurs with the transfer of self-fruitfulness from related wild species the cultivated almond. While an extensive wild almond and related germplasm have been well documented in the literature of the past century, this information remains dispersed and often not widely accessible owing to its publication in treatises and journals of limited distribution. The goal of this volume is to bring together a comprehensive characterization of almonds and their related species. More than 40 species have been documented within this group, demonstrating extensive morphological variation representative of their diverse geographical origins. Most species are endemic to Central and Western Asia, with the most being found in Iran. The Zagros Mountains in southwestern Iran possess an exceptionally wide diversity of almond species and are widely considered the site of origin for the

progenitors of the cultivated almond. Native almond species have also played important social, economic, and ecological roles in their native regions. The fruit and kernel have historically been an important source of food (even bitter kernels can be made edible by processing), as well as essences and oils used for making products ranging from medications to cosmetics. The wood is durable and fine-grained, making it valued for multiple uses, from woodworking to producing high-quality charcoal. In many regions, endemic almond species continue to play important ecological roles, including controlling erosion and acting as greenbelt filters for urban areas. The diverse germplasm possesses numerous traits of value for crop improvement, including improved resistance to biotic (pests and diseases) and abiotic stresses (drought, frost, and winter damage), as well as modified tree architectures and bearing habits. There also exists a long tradition for the use of this native germplasm as rootstocks for almond and other *Prunus* crops, particularly where tree size control and improved drought resistance are desired. Other traits useful for crop improvement include later flowering for frost avoidance, self-fruitfulness, and precocious-cropping. Accurate assessment of genetic diversity and breeding value, however, depends upon a clear understanding of species properties and relationships. Gametic self-incompatibility in most species results in obligate outcrossing, enhancing both morphological and genetic variability within species. Because strong interspecific breeding barriers are not commonly present, considerable interspecies hybridization and subsequent introgression can also be found in the wild. While the resulting genetic and developmental uniqueness of almond and its wild relatives has resulted in it being classified in the genus *Amygdalus* in most European and Asian studies, this study also includes the more recent APG IV system of classification placing them within the genus *Prunus*. To maintain accuracy, the classification presented in the original publication will be the classification presented in this volume.

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Chapter 1

An Introduction to Almond Species and Their Origins



In addition to their historical importance as food crops, almond species are becoming increasingly utilized in landscaping, ecological restoration, and reforestation. Almond improvement is currently limited by restricted breeding germplasm (Gradziel et al. 2001), and genetic improvement programs are increasingly turning to wild germplasm as sources of improved quality, productivity, and resistance. This germplasm is also enabling the dramatic transformation of traditional cropping systems, as with the recent transfer of self-fruitfulness from related wild almond species to normally self-sterile cultivated almonds (Gradziel 2021). While the presence of an extensive wild almond and related species germplasm has been documented in the literature over the past century, most information remains dispersed and not generally accessible owing to its frequent publication in treatises and journals of limited distribution. This monograph brings together a comprehensive characterization of almonds and their related species, including the readily cross-hybridized peaches and plums, which are also within the section *Euamygdalus*. Because it represents the only comprehensive source of information on this germplasm, this monograph is presented as a basic reference that may be of interest to researchers in both the basic and applied plant and ecological sciences.

While a rich genetic diversity is crucial for the successful domestication of a plant species, that success often leads to increased commercial acreage and a loss of native habitats with consequent reductions in the level of overall genetic diversity (Doebley 1989). This accelerating trend highlights the need to identify, capture, and maintain as much useful genetic diversity as possible before it is lost. Because the cultivated almond, like most of its wild almond relatives, is self-incompatible and, therefore, an obligate outcrosser, genetic variability is high even in progeny from a cross between two cultivars. As cultivars become more related, genetic options for future improvement become increasingly limited by the negative effects of inbreeding. In contrast to genetic variability, genetic diversity is enhanced by bringing in germplasm from diverse sources, which maximizes opportunities for new trait discovery while minimizing inbreeding (Goldstein and Schlotterer 1999). An

understanding of the genetic and evolutionary relationships between different species is thus important for determining the final breeding value. Similarly, a more comprehensive, systematic analysis improves our understanding of both the mechanisms and opportunities for gene flow under natural selection, facilitates more accurate taxonomic classifications, and facilitates the identification of high-value core germplasm for specific objectives (Arzani 2004). This germplasm is particularly interesting in this regard because the wild almonds are classified within the genus *Prunus* largely on the basis of genetic similarities, including high degree of synteny with peach and its wild relatives, while the classification within the subgenus *Amygdalus* is based on the distinctly different growth habits and final plant architectures of almond species when compared to peach species. Thus, it represents an intriguing example of the evolution of distinctly different phenotypes based on very similar initial genotypes.

The Origin of Almonds

Wild almonds in Central Asia include more than 30 named species extending across a large geographical distribution and adapted to a wide range of ecological conditions from deserts to alpine regions, resulting in an exceptionally high genetic diversity driving the evolution of multiple ecotypes, subspecies, and strains. Natural populations extend from the Levant to Turkmenistan and Southwest Asia, including the slopes of the Tian Shan Mountains of Uzbekistan and Tajikistan, and the Hindu Kush mountains of Afghanistan (Kester and Gradziel 1996; Grasselly and Duval 1997). The center of diversity appears to be in Iran, where 21 species have been cataloged in semiarid forests, 17 species in dry and desert forests, 6 species in dry and subtropical forests, and 3 species in semi-humid forests (Javanshir 1976). No wild almond species have been reported in humid forest ecosystems typical of the closely related wild peach species *Prunus davidiana*, *P. mira*, and *P. kansuensis*.

Natural sweet-kerneled populations of the *Prunus communis*, which is considered a progenitor of domesticated almonds, have been reported in two separate regions (Vavilov 1930; Denisov 1988). One occupies the slopes of the Kopet Dagh Mountains in central Asia near the present-day borders of Iran, Turkmenistan, and Tajikistan. The second has been reported on the slopes of the Tian Shan Mountains between Uzbekistan and Xinjiang, China. This species is well adapted to the mild winter and dry, hot summer conditions of these regions, possessing the favorable traits of low chilling, early bloom, rapid early shoot growth, deep penetrating root systems, and high tolerance to summer heat and drought. The phenotypic range of *P. communis* closely resembles that of present-day cultivated almonds (Kester and Gradziel 1996). Because most native stands of *P. communis*, including the naturally bitter-kerneled types, lie further west of the Tian Shan mountains, the Xinjiang trees are now thought to be remnants of very early and possibly prehistoric plantings from early Silk Road trading. The more ecologically diverse western *P. communis* germplasm is divided into two eco-geographical strains or subspecies (Zohary and Hopf 2000). Subspecies *spontanea* is naturally found in Mediterranean regions with

an annual rainfall of 350–800 mm and typically has larger wild-type trees. This subspecies more closely resembles modern cultivated almonds in the morphology of leaves, flowers, and growth habits, and climatic responses, including a tendency for early bloom. Subspecies *microphylla* represents a more xerophyte group commonly found in arid steppe or pseudo steppe forests of central Asia, developing smaller leaves, fruits, and tree sizes relative to the Mediterranean subspecies.

There are several hypotheses concerning the origin of almonds. Most propose that the cultivated almond is derived from sweet-kernelled genotypes of naturally bitter *P. communis*, possibly involving hybridization with other species. Sweet-kernelled stands may have been the result of human selection, in which trees with the sweet kernels are selected, and the bitter kernel trees are eliminated (Kovalev and Kostina 1935; Kester and Gradziel 1996), suggesting an origin of cultivated almonds involving prehistoric human intervention and thus not a natural species (Evreinov 1958; Kester and Gradziel 1996). Delplancke et al. (2013) believe that the genetic diversity of contemporary domesticated species is favored by both natural and human-driven processes. Most historic as well as modern cultivars are heterozygous for the bitter/sweet allele as this confers resistance to herbivory in the leaves where bitterness is dominant as well as sweetness in the kernel where the bitter trait is recessive. Consequently, most seedlings from sweet-kernelled selections will segregate for homozygous bitter-kernelled trees. In historical and even modern seedling orchards in the Mediterranean and Central Asian production regions, most homozygous bitter seedlings are top-worked to sweet-kernelled types, though some are retained for bitter kernel production to be used in manufacture of amaretto-flavored foodstuffs such as marzipan.

It has also been suggested that *P. communis* is itself a hybrid between wild almond species that have sweet-kernelled types, such as *P. bucharica*, *P. fenzliana*, and *P. kuramica* (Crossa-Raynaud and Grasselly 1985) or *P. bucharica*, *P. fenzliana*, and *P. ulmifolia* (Vavilov 1930; Kester and Gradziel 1996). In this scenario, sweet-kernelled types originate as relatively rare mutations but would then be maintained by humans and possibly natural selection (Kester and Gradziel 1996). *P. kuramica*, which is morphologically similar to cultivated almonds, is native to Afghanistan and Pakistan. It can tolerate dry conditions (xerophyte) better than cultivated almonds (Kester and Gradziel 1996). Both *P. bucharica* and *P. fenzliana* develop relatively large fruits compared to the other wild species and appear to be more closely related to cultivated almonds (Grasselly and Duval 1997). While a distinct interspecies origin of cultivated almond has not been unequivocally demonstrated (Ladizinsky 1999; Bortiri et al. 2002), natural interspecies hybridization and subsequent gene flow with cultivated almonds have been documented (Grasselly 1976; Denisov 1988; Grasselly and Duval 1997). For example, the cultivation of almonds in Mediterranean regions where *P. webbii* occurs has resulted in natural interspecies hybridization and subsequent gene flow leading to the transfer or introgression of self-compatibility from *P. webbii* to cultivated almonds (Serafimov 1975). Recurrent selection for market-desirable kernel types has resulted in self-fruitful selections such as the heirloom cultivar *Tuono*. Similarly, close inspection of regional almonds being sold in many Central Asian bazaars often finds mixtures containing the distinctly scribed endocarps characteristic of interspecies origins (Fig. 1.1).

Fig. 1.1 Mixed almonds in a bazaar in Georgia. (Maghradze and Bobokashvili 2006)



The edible, sweet-kerneled almond, thus, may represent more a market type with contributions from multiple species rather than being a single, distinct species. In fact, in central Asia, it is often referred to as “badam,” a term that generally refers to the edible seed from a range of *Prunus* species, including wild almonds as well as peach and apricot.

Almonds have been grown in the Middle East since ancient times, with the earliest historical evidence of almond production being found in Babylonia. In the Sassanian era (224–651 AD), almond cultivation in Iran became commonplace. Almond domestication is thought to have first taken place from about 2000 BC to 3000 BC, most likely in the early Bronze Age. Archaeological evidence supports an extensive collection by earlier cultures from wild almond stands with possible selection within the stands for the most desirable, sweet-kerneled types, resulting in the suggestion by Zohary and Hopf (2000) that almonds were the first species of fruit trees to be cultivated in the old world. Because of their high tolerance to stress, almonds tended to be cultivated in the more marginal sites as a low-input but often low-return crop (Grasselly 1972). Significantly, early almond production was located adjacent to ancient major trade routes (such as the Silk Road), leading to its rapid dissemination throughout Central and Southwestern Asia, including China, Northwest India, Northern Pakistan, Iran, Turkey, Syria, and Israel. Browicz (1974) described how *P. communis* probably reached Syria, Lebanon, and Jordan via Iran, Caucasus, and Turkey (Fig. 1.2). Vezvaei (2003) documents a particularly high polymorphism for almonds in Iran, suggesting that it is a center of diversity and possibly a center of domestication for this crop.

Almonds were subsequently spread by the Phoenicians, Greeks, and Romans to all parts of the Mediterranean, including Greece, Italy, France, Spain, and Portugal, as well as North Africa, including Tunisia and Morocco. In the 1700s, almonds were taken to North America during the Spanish colonization of California, with extensive commercial almond cultivation beginning in western North America in the mid-eighteenth century (Kester and Gradziel 1996). Subsequent distributions extended to South America, South Africa, and Australia, utilizing mainly hard-shell cultivars originating from Spain, Italy, and Jordan, while the origin of soft-shell almonds is primarily from California and the Languedoc region of France (Woolley et al. 2000) (Fig. 1.3).



Fig. 1.2 Distribution of Almond via Iran (1), Caucasus (2), and Turkey (3) to Syria, Lebanon, and Jordan. (Rahemi 2015)

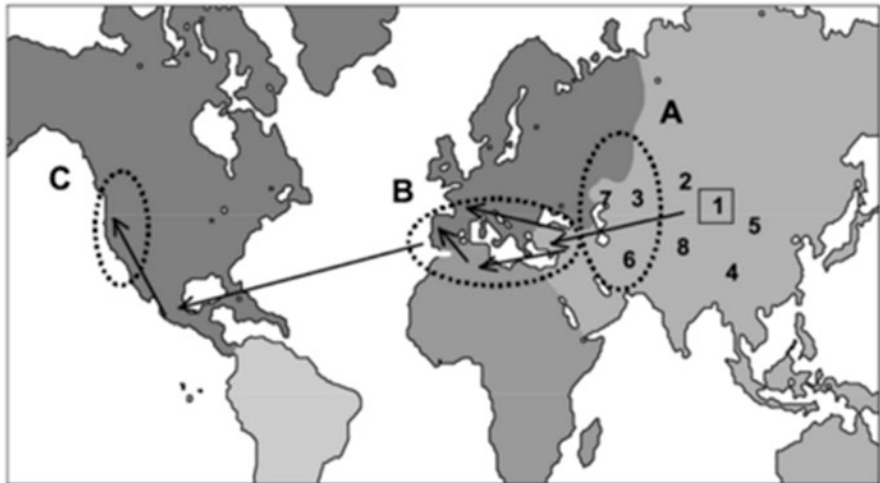


Fig. 1.3 Map of the world showing the origin of almonds, *Prunus dulcis* (1), *P. bucharica* (2), *P. fenzliana* (3), *P. davidiana* (4), *P. persica* (5), *P. scoparia* (6), *P. webbii* (7), and *P. argentea* (8). The dissemination routes for the cultivated almond [→], and the three main areas for diversification and cultivation of almonds [Asiatic (A), Mediterranean (B), and Californian (C)]. (Martínez-Gómez et al. 2007)

Among the different species of the genus *Prunus*, almonds are most closely related to peaches, so they have been placed in the same subgenus “*Amygdalus*.” During their recent evolution, almonds and peaches have been separated by the rise

of the Himalayan Mountains and Tibetan Plateau occurring approximately 10 million years ago. Consequently, despite their high genomic similarities, peach species became adapted to the more humid climates of East Asia, while the almond species became adapted to the increasingly xerophytic environments of Central and Southwest Asia (Watkins 1979; Kester and Gradziel 1996), resulting in distinct developmental morphologies.

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