Almond (*Prunus dulcis*) Breeding

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1 Introduction

An adaptation to harsh climates combined with an ability to develop a deep and extensive root system has allowed cultivated and wild almond to exploit a wide variety of ecological niches in its ancestral range in central Asia extending from the Takla Makan desert in western China to the Mediterranean (Kester et al. 1991; Ladizinsky 1999). Almond is also well adapted to mild winter and dry, hot summer conditions due to its low chilling requirement for early bloom, rapid early shoot growth, and high tolerance to summer heat and drought. It is the earliest temperate tree crop to bloom, which limits production to areas relatively free from spring frosts. Because almond is self-sterile, it requires cross-pollination that further acts to promote genetic variability and, therefore, adaptability to new environments.

Commercial production is often limited by the need for cross-pollination in orchard systems, particularly in areas where spring storms can reduce both flowering duration and activity of required insect pollinators. A high susceptibility to fungal and bacterial diseases of the blossoms, leaves, branches, and fruits also reduces production in areas with rain and/or high humidity during the growing season (Kumar and Uppal 1990; Ogawa and English 1991). Similarly, excessive moisture in the root zone can result in tree losses due to root rots or asphyxia.

1.1 Origin and History

Early researchers proposed that cultivated almond resulted from selection from within a species listed originally as *Amygdalus communis* L. (syn. *Prunus communis* Archang.) based on studies of two natural populations originally

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identified as *A. communis* and containing large numbers of sweet seeded individuals rather than the bitter kernels typically found in the wild (Watkins 1979). One population is located in the Kobet Dag mountain range in central Asia between present-day Iran and Turkmenistan, and the second population occurs on the lower slopes of the Tian Shan mountains between Kyrgyzstan and western China. The natural range of *A. communis* was proposed to have extended across Iran, the Transcaucausus, and eastern Turkey, and into present-day Syria, and thus overlapped with known sites of early almond cultivation (Denisov 1988; Kester et al. 1991). According to this view, the distinction between cultivated and wild forms gradually disappeared with direct and indirect human selection. However, because the purportedly natural sweet-kernelled populations closely resemble the phenotypic range of present-day cultivated almonds, it has recently been suggested that the Kobet Dagh and Tian Shan populations are, in fact, more recent remnants or escapes from later domesticated or semidomesticated orchards (Ladizinsky 1999). The emerging consensus is that cultivated almond represents a generalized, fungible kernel phenotype, possibly derived from *P. fenzliana*, but with contributions through natural interspecific cross-hybridizations with a range of related species occurring naturally within this range (Fig. 1), including *P. bucharica, P. kuramica,* and *P. triloba* (Godini 2000; Grasselly and Crossa Raynaud 1980; Kester et al. 1991; Socias i Company 2002).

A subsequent and widespread dispersal of 'cultivated' almonds occurred in three stages: Asiatic, Mediterranean, and Californian. The Asiatic stage included the initial domestication and the subsequent spread throughout central and southwestern Asia often along major prehistoric trade routes. The range centers on present-day Iran extending east to western China, northwest India, northern Pakistan, northwest through Turkey, and southwest into the uplands and deserts of central Israel and Syria. Almonds are reported in Hebrew literature as early as 2000 BCE. Their culture continues to the present time within the Asiatic region, where in many areas, almonds are grown under dryland, subsistence agricultural practices similar to those used thousands years ago.

In the Mediterranean stage, almonds appear to have been brought into Greece prior to 300 BCE, eventually being introduced to all compatible areas of the Mediterranean. Initial introductions may have come from the early ocean trading Phoenicians and Greeks during establishment of colonies in Sicily and other Mediterranean sites (Bacarella et al. 1991). Cultivation typically occurred within 80 km of the Mediterranean coast extending onto the slopes of river valleys as well as the interior areas in Spain. Subsequent introductions occurred in 500–600 CE with the conquest of North Africa by Arabs who also brought almonds into southern Spain and Portugal. Two thousand years of continuous cultivation in the Mediterranean basin has concentrated almond plantings into specific regions where well-defined seedling ecotypes have evolved. A tolerance to drought and high susceptibility to soil moisture placed almonds in a mixed culture system with olives, carob, and other desert-adapted crops. Almonds were typically found at higher elevations on well-drained slopes to avoid spring frosts. In these more

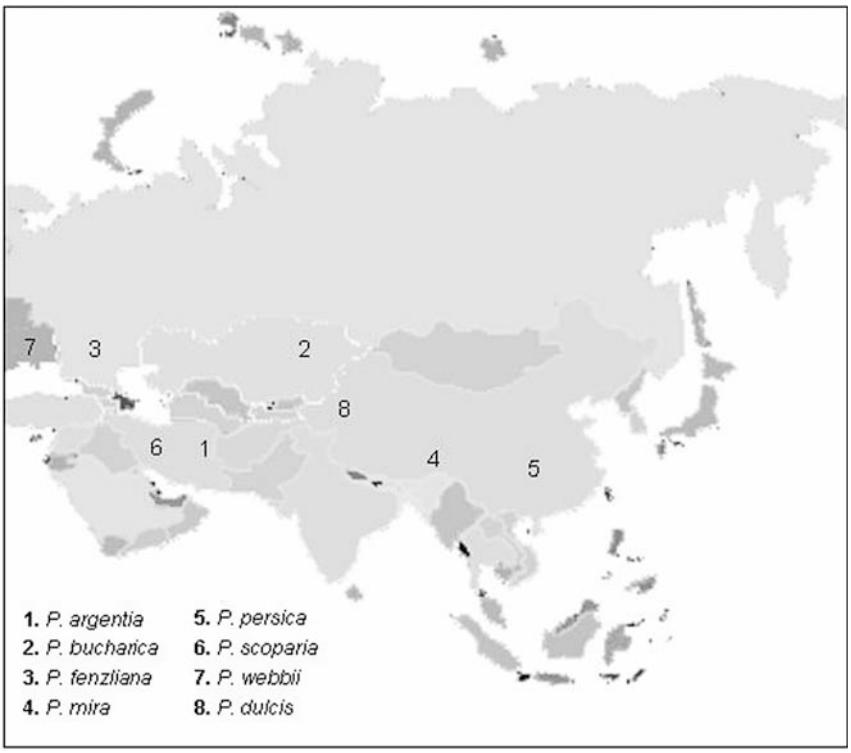

Fig. 1 Map of Asia showing origin of selected almond species

marginal environments, cultural practices evolved which minimized inputs of labor, fertilizers, and use of supplementary water. Locally adapted seedling populations eventually led to a number of local selections adapted to very specific climatic and culture conditions. Selection toward greater local adaptation appears to have been augmented by a more recent introgression of genes from nearby wild almond species. Godini (2000) and Socias i Company (1990) provide evidence for the introgression of self-compatibility and morphological features from *P. webbii* in the development of commercially important cultivars along the northern shore of the Mediterranean Sea.

Both natural- and human-directed*s* selections appear to have occurred both in parallel and in conflict. For example, presence of the bitter kernel gene would be desirable in the wild as it confers resistance to herbivory but would be undesirable for human consumption. Despite its commercial undesirability, most European cultivated almonds are heterozygous for bitterness and many open pollinated seed-derived local land races typically segregate for the bitter kernel trait (Grasselly 1972). The need to graft-over bitter seedlings within these

populations eventually led to selection of local vegetative clones, which subsequently became characteristic of these regions (Bacarella et al. 1991).

The Californian stage initially began as an extension of Mediterranean culture, utilizing a hard-shelled germplasm originally brought from Spain. Later, soft-shell types more compatible for California were introduced from France. High-input orchard practices, however, soon differentiated Californian production from that of Europe and Asia. Important California cultural changes included the movement of almond production from more marginal coastal sites to the very productive Central Valley, the development of new rootstocks and orchard management practices for these highly productive sites, the selection of consistently high-yielding cultivars, and the standardization of markets based upon a relatively few cultivar types. The combination of highly adapted cultivars and rootstocks, favorable soil and climate, abundant water, and effective management has given California growers the highest productivity in the world. Production per hectare continues to show upward trends with yields surpassing 4 MT per hectare presently possible with some cultivar/site combinations.

1.2 Production

The combination of high productivity with extensive plantings has made California the major producer of almonds for commerce with approximately 453,000 MT of nut meats being produced on over 230,000 ha in 2004 (Table 1). Other major almond-producing regions include the European countries bordering the Mediterranean Sea.

Spain, the second leading producer, has a cultivated area of 567,000 ha, producing approximately 26,000 MT in 2004 under primarily low to medium input agriculture. The remaining world production comes from about 20 countries including Italy, Turkey, Greece, and India. Limited almond production extends into the Balkan Peninsula including areas of Bulgaria, Romania, and Hungary. A third area exists in central and southwestern Asia including Syria, Iraq, Israel, Iran, Ukraine, Tajikistan, Uzbekistan, Afghanistan, and Pakistan, extending into western China.

Table 1 Commercial production of almonds in major producing countries (Almond Board of California 2005)

Country	Production (metric ton)
California (USA)	453,000
Spain	26,000
Turkey	14,000
Greece	10,000
Italy	5,000
India	1,000

Many almond species are native to these Asiatic regions where almond growing is often under dryland, low-input culture. Significant almond production also occurs in the southern hemisphere countries having a Mediterranean-type climate including regions in Australia, central Chile, Argentina, and South Africa.

1.3 Uses and Nutritional Composition

The almond kernel is consumed either in the natural state or processed. Because of its good flavor, crunchy texture, and good visual appeal, it has many important food uses (Rosengarten 1984). As an ingredient in many manufactured food products, kernels may be roasted dry or in oil followed by salting with various seasonings (Schirra 1997; Woodroof 1979). The processed kernel is used either blanched or unblanched. Blanching removes the pellicle ('skin') using hot water or steam. Large amounts of kernels are combined with chocolate in confectionery. Almond kernels can be sliced or diced to be used in pastry, ice cream, breakfast cereals, and vegetable mixtures. The kernels are also ground into paste to be used in bakery products and in the production of marzipan. The flavor and texture of almonds can be intensified or moderated through proper selection of cultivar, origin, moisture content, and processing and handling procedures (Kester et al. 1993).

Variation in amygdalin content accounts for some cultivar flavor differences, particularly the distinct amaretto flavor common in certain Mediterranean almonds (Dicenta and García 1993b; Vargas et al. 2001). Californian cultivars had amygdalin contents ranging from 0.33 to 0.84% with only 'Peerless' outside this range at 1.75% (dry weight). In contrast, the Italian cultivars varied from 0.73 to 1.95% with only two cultivars below that range (Schirra 1997). Even higher amygdalin levels will result in bitter almond seeds, which are often blended with sweet.

To obtain the bitter reaction, the substrate amygdalin and a beta-glucosidase enzyme must come into contact through damage to and lysis of the cells. Bitterness results from the hydrolysis of the glucoside amygdalin by a beta-glucosidase enzyme, which produces benzylaldehyde (that confers the 'cherry' or 'amaretto' flavor) and cyanide (which is poisonous) (Kester and Gradziel 1996). Benzaldehyde is also known in the chemical and flavoring industries as 'oil of bitter almond' because of its preponderance in bitter rather than sweet almonds. This trait is typical of the wild almond species where it protects the seed against herbivory.

Almonds are among the most nutrient dense of all tree nuts (Kendall et al. 2003). They are a very good source of essential fatty acids, vitamins, and minerals (Saura-Calixto et al. 1981; 1982) (Table 2). Raw almonds are one of the best plant sources of protein. While certain nut storage proteins can pose

Table 2 Nutrient composition of the almond kernel per 100 g fresh weight of edible portion (Adapted from Socias i Company et al. 2007)

Nutrient	Value
Energy	578 kcal
Protein	21.26 g
Carbohydrate	19.74 g
Fiber, total dietary	11.8 g
Glucose	4.54 g
Starch	0.73 g
Calcium	248 mg
Magnesium	275 mg
Phosphorus	474 mg
Potassium	728 mg
Sodium	1 mg
Folate, total	29 μg
Vitamin E	25.87 mg
Saturated fatty acids	3.88 g
Monounsaturated fatty acids	32.16 g
Polyunsaturated fatty acid	12.21 g

an allergenic health threat to consumers, Sathe et al. (2001) found no significantly elevated risk in a range of cultivated almonds as well as interspecies hybrids. Almonds are also one of the best natural sources of vitamin E (Sabate and Haddad 2001), which is believed to play a role in preventing heart disease, certain kinds of cancer, and cataract formation (Kodad et al. 2006). A single ounce of almonds (approximately 20–25 kernels) contains 37% of the recommended daily value of vitamin E, 21% of magnesium, and 15% of the recommended daily value of phosphorus. Almonds also represent a convenient source of folic acid and fiber (Schirra 1997; Vezvaei and Jackson 1996). Historical uses of sweet and/or bitter almond ointment included the treatment of asthma and pattern baldness; it was also used as a soothing salve for burns.

The almond kernels are also a source of high-quality oil (Abdallah et al. 1998; Garcia-López et al. 1996; Kodad et al. 2005). The oil, which can constitute over 50% of the kernel dry weight, is primarily composed of the more stable oleic acid making it desirable from ancient times to the present for use as a base for various ointments and pharmaceuticals. The high levels of this monounsaturated fat may be partly responsible for the observed association between frequent nut consumption and reduced risk of coronary heart disease (Fulgoni et al. 2002; Lovejoy et al. 2002). Recent evidence has suggested that the incidence of deaths due to coronary heart disease, hypertension, congestive heart failure, and stroke is decreased in people who eat a serving of nuts several times per week (Socias i Company et al. 2007).

Because of their high lipid content (approximately 50–55%), almond kernels are a concentrated energy source (Fraser et al. 2002). The oil is primarily mono-unsaturated, being approximately 65% oleic and 30% linoleic acid, which results in an agreeable supple, buttery flavor, high nutritional value, as well as long-term stability in storage (Fulgoni et al. 2002; Garcia-López et al. 1996;). The hull, which is analogous to the flesh of the closely related peach, contains about 25% sugar and is utilized as a livestock feed. A thorough review of almond nutritional and food quality traits, including opportunities for their genetic manipulation, has recently been compiled by Socias i Company et al. (2007).

2 Botany

While the cultivated almond and its close relatives share basic botanical features and developmental patterns, particularly in the area of reproductive biology, the divergent selection pressures of the wide range of ecological niches occupied have resulted in an extensive variability in final tree and nut form (Felipe and Socias i Company 1992; Niklasson 1989). Within this broad geographical region, extending from the Levant to China, the botanical structure defining commercial quality was a fungible or marketable kernel. High tree productivity, as it increased plant stress, would be a liability in many of the marginal, dryland environments of both ancient and contemporary plantings within these regions. In these harsh environments, primary selection was on tree survival with some level of consistent kernel production regardless of final tree form or physiological pathways. The resulting phenotypic variability offers a wealth of useful traits for cultivar improvement. The divergent development patterns based on unusually similar genomes also offer unique opportunities for the study of the fundamental regulation of plant development.

2.1 Taxonomy

The almond fruit is classified as a drupe with a pubescent skin (exocarp), a fleshy but thin hull (mesocarp), and a distinct hardened shell (endocarp). The hull undergoes limited enlargement during development, later becoming dry and leathery and dehiscing at maturity (Fig. 2). The mature endocarp ranges from hard to soft and papery, depending upon the genotype. Horticulturally, almonds are classified as a 'nut' in which the edible seed (the kernel or 'meat') is the commercial product. The kernel includes an embryo surrounded by the pellicle. Within the *Prunus* genus, the almond is closely related to peach (Felipe 1975). While almond evolved in the xerophytic environment of central and southwest Asia, the peach evolved in the more humid climates of eastern Asia, separated from the almond by the uplifting of the central Asian Massif.

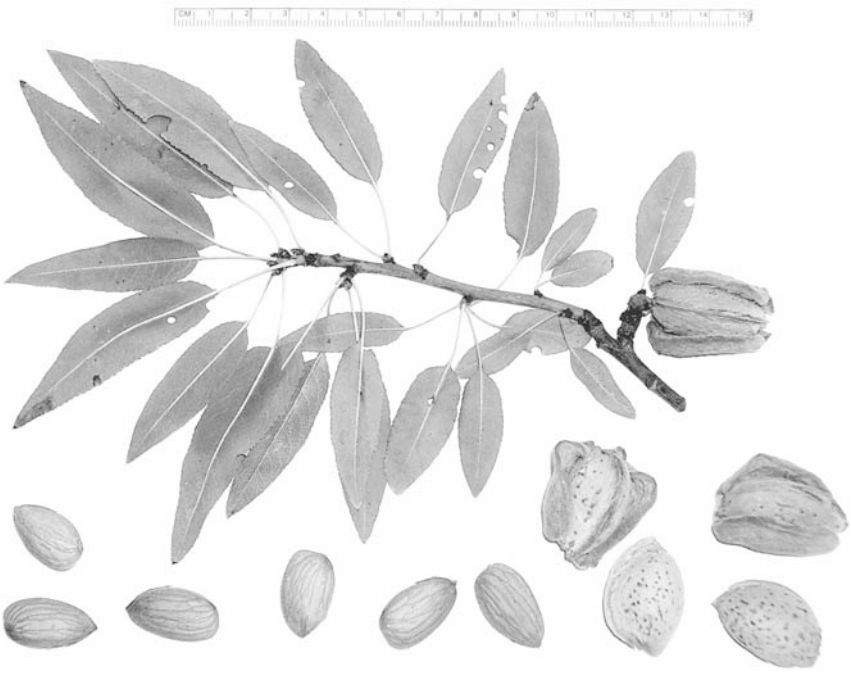

Fig. 2 Cultivated almond shoot showing leaf, fruit, and kernel morphology

Wild populations of almond species representing a wide range of morphological and geographical forms have evolved throughout central and southwestern Asia. Some of the more than 30 species described by botanists may represent subspecies or ecotypes within a broad collection of genotypes adapted to the range of ecological niches in the deserts, steppes, and mountains of central Asia (Grasselly 1972). Browicz (1969) separated almond species into two subgroups: Amygdalus (leaves conduplicate in bud and 20–30 or more stamens) and Dodecandra (leaves convolvulate in bud and fewer than 17 stamens). The most northeasterly group located in western China and Mongolia includes *P. mongolica, P. pedunulata*, and *P. tangutica (P. dehiscens)*, the latter probably in section *Chamaeamygdalus*. The remainder occupies a more or less contiguous area in west central Asia. Almonds in the most northern range include species in section *Chamaeamygdalus* and extend from the Balkan Peninsula to the Altai Mountains. The most southern and xerophytic groups include species in the *Spartiodes* section, which can have leafless slender shoots, and the *Lyciodes* (Dodecandra) section, which are very dwarfed and thorny. Species in the section *Euamygdalus* resembles cultivated almonds and includes many species extending from central Asia to southern Europe (Table 3) as well as the peaches *P. persica, P. mira,* and *P. davidiana*. The chromosome number

Table 3 Botanical relationship of *Prunus* species in subgenus *Amygdalus*

Almond group
Section *Euamygdalus* Spach
Prunus dulcis (Miller) D.A.Webb
P. bucharica Korshinsky
P. communis (L) Archangeli
P. fenzliania Fritsch
P. kuramica Korchinsky
P. orientalis (Mill.), syn. *P. argentea* (Lam)
P. kotschyi (Boissier and Hohenm.(Nab) and Rehd.)
P. korschinskii Hand-Mazz.
P. webbii (Spach) Vieh.
P. zabulica Serifimov
Section *Spartioides* Spach
P. scoparia Spach
P. spartioides Spach
P. arabica Olivier
P. glauca Browicz
Section *Lycioides* Spach
P. spinosissima Franchet
P. turcomanica Lincz.
Section *Chameamygdalus* Spach
P. nana (Stock)
P. ledebouriana Schle.
P. petunnikowi Lits.
P. tangutica Batal.(syn. P. dehiscens) Koehne
Peach group
P. persica (L.) Batsch.
P. mira Koehne
P. davidiana (Carriere) Fransch.

of *P. dulcis (P. amygdalis),* as well as *P. fenzliana, P. nana (P. tenella), P. bucharica, P. kotschyi,* and *P. scoparia*, is $2n = 16$, which is the same as peach *P. persica* (Kester et al. 1991).

2.2 Interspecific Hybrids

While several reports have documented recovery of genes for self-compatibility from related almond species through either natural or controlled crosses (Denisov 1988; Felipe 2000; Gradziel and Kester 1998; Socias i Company and Felipe 1988, 1992), only Rikhter (1969), Grasselly (1972), Denisov, (1988), Kester et al. (1991), and Socias i Company (1990) have previously reported the use of wild species germplasm to create improved almond cultivars. The

historical use of these species and their hybrids as almond rootstocks would facilitate subsequent introgressions. The use of wild species directly as a rootstock for dryland almond has been widely reported, including *P. spartioides* in Iran, *P. bucharica* and *P. fenzliana* in Russia, *P. webbii* in Turkey, and *P. fenzliana, P. bucharica, P. kuramica, P. argentea, P dehiscens*, and *P. kotschyi* at lower incidence in these (Fig. 1) and nearby areas (Gradziel et al. 2001a; Denisov 1988; Grasselly 1972; Rickter 1969; 1972).

Recently, crosses between almond and related species have been readily achieved under controlled conditions (Gradziel and Kester 1998; Gradziel et al. 2001a; Gradziel 2003). While a wide variability in tree and branch architecture results, leaf and nut phenotypes of resultant hybrids are typically intermediate to the parents (Fig. 3). Interspecific crosses between related species (mainly *P. persica* × almond but also *P. webbii* × almond) have been used for almond rootstock breeding in France, USA, Spain, and Yugoslavia (Gradziel et al. 2001b; Denisov 1988; Grasselly 1972; Rickter 1969; 1972; Vlasic 1976). In addition, Browicz and Zohary (1996) and Ladizinsky (1999) have reviewed evidence for a high level of spontaneous interspecific hybridization in the wild between species with overlapping ranges. Surprisingly, the most promising

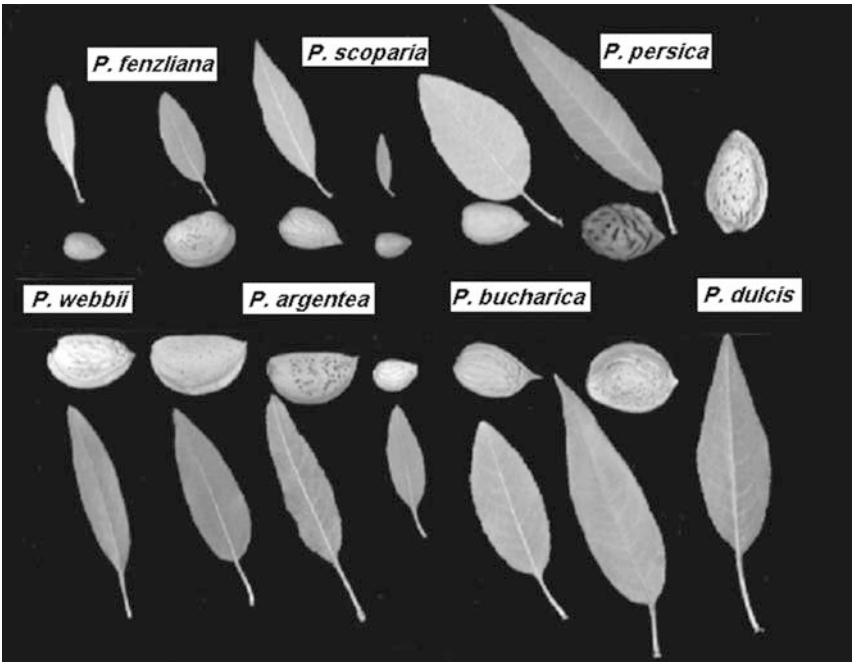

Fig. 3 Leaf and nut morphologies of parent species (*top*) and hybrids with cultivated almond (*bottom*). Typical cultivated almond nut and leaf shown at right

sources of new genes may be the more developmentally distinct peach group including *P. persica, P. mira*, and *P. davidiana*. Rehder (1940; 1967) has placed all of the species examined in this survey in the genus *Prunus*. *P. dulcis* (cultivated almond), *P. persica* (cultivated peach), *P. mira, P. argentia, P. dulcis, P. bucharica,* and *P. fenzliana* are placed in the subgenus *Amygdalus*, section *Euamygdalus*; *P. scoparia* is placed in the section *Spartiodes*; and *P. webbii* placed in the section *Lycioides* (Table 3). However, many Mediterranean and Central Asian researchers prefer the classification of Browicz and Zohary (1996) where *P. persica, P. mira*, and *P. davidiana* are in the genus *Prunus*, while almond and the other almond-like species discussed here were placed in the genus *Amygdalus*. While acknowledging the easy hybridization between almonds and peaches and so the high level of synteny between these genomes, these researchers argue that the divergent evolution of almonds in the harsh climates of central Asia and peach in the temperate to subtropical climates of southeastern China have led to dramatically different growth and development patterns. From an ecological and even taxonomic perspective, these wide divergences suggest their placement in separate genera. Almond and peach thus represent a unique situation in crop plant genetics, where very similar genomes are expressed as very different plant forms. This genome–phenotype disjunction may prove useful for the elucidation and eventually manipulation of the recently recognized epigenetic (i.e., nongenomic) mechanisms, which are now recognized to have profound effects on fundamental plant developmental pathways, and therefore final form and function.

2.3 Reproductive Biology

Almond produces a typical perigynous self-incompatible Prunus flower. Honeybees, foraging for pollen or for nectar secreted at the base of the flower, are important pollinators (Thorp and Roper 1994). Flowers of different cultivars and species may differ in petal size, shape, color, number of stamens, and arrangement and length of anthers relative to stamens. The number of stamens may vary from 20 to about 40 with the usual number being 30–33. The distributions of stamen number within seedling populations from parents of different stamen number indicate quantitative inheritance with a tendency toward dominance of larger numbers. Although the usual pistil number is one, some genotypes such as`Eureka' tend to produce two, which may result in a double fruit. Two flowers can sometimes be produced within the same flower bud with similar results. The structure of the pistil and style also varies. Some styles are straight and elongated, extending above the anthers by petalfall. In other individuals, the stigmas and the anthers are approximately at the same level, a condition associated with increased chances for self-pollination.

Flower differentiation takes place during summer, primarily in August, and floral development continues into the fall and winter (Polito and Micke 1994). Time of flowering is one of the most important adaptive traits of almond as it determines vulnerability to spring frosts. Flowering time is determined by chilling requirements to overcome dormancy and subsequent heat requirements for subsequent bud growth and development. Actual timing of bloom can vary from year to year depending upon the temperature patterns before and during bloom (DiGrandi-Hoffman et al. 1994). In general, the sequence of bloom among different cultivars tends to be fairly constant, but relative bloom time between specific cultivars can sometimes be reversed because of differing requirements for initial chilling or subsequent heat. This relationship is important commercially since it is desirable to have a cultivar flower just before the high-value cultivar in order to maximize its cross-pollination and so yield. For this reason, bloom time is often given relative to a high-value cultivar. In California, 'Nonpareil' is commonly used, whereas in the Mediterranean area, 'Marcona' is frequently the standard.

The cultivated almond as well as most almond species expresses gametophytic self-incompatibility, which discourages self-fertilization, favors cross-pollination, and thus maintains genetic variability within seedling populations. Genetic control of pollen–pistil self-incompatibility is through a single gene (S), which exists in a series of alleles including an allele for self-compatibility. Each diploid genotype carries two alleles of the series. Pollen grains, which have a haploid genome, are unable to fertilize a pistil possessing the same allele. Pollen genotypes with the same S-alleles as the pistil show self-incompatibility as well as cross-incompatibility with other cultivars with the same S-allele. Cross-incompatibility groups (CIGs) have been identified and incompatibility alleles have been assigned to many of them (Boškovic et al. 2003; Channuntapipat et al. 2003; López et al. 2004; Tamura et al. 2000). These groups are important because they guide the selection of cultivar combinations used in orchard planting and provide important gene markers for pedigree studies. CIGs have now been identified for all major California cultivars (Barckley et al. 2006).

Self-fruitfulness refers to the ability of a plant to be fertilized from self-pollen. This competence requires a combination of both self-compatibility and successful self-pollination. Different degrees of self-compatibility exist (Gradziel et al. 2002b). Low pollen tube and ovule growth rates associated with certain genotypes can also decrease the probability of successful fertilization.

Following fertilization, the growth of the fruit, seed, and embryo follows the typical three stages of development in which the pericarp, seed, and nucellus develop during stage I, the endosperm and embryo enlarge during stage II, and the dry weight of the embryo increases during stage III. Time of nut maturity is an important commercial trait. Physiological processes, which accompany almond fruit ripening, include dehiscence of the hull or mesocarp, hull-split, fruit abscission, and dehydration or the loss of moisture in the hull and nut. The entire process of hull and nut maturation and drying may require 2–6 weeks to

complete. Usually maturity is most reliably characterized by the initiation and progress of hull splitting. The dates for the initiation of 5–10% splitting and the completion of splitting are useful criteria when comparison is made to standard cultivars. Moisture stress can accelerate hull splitting, but adequate moisture is required for the hull to ripen properly. If splitting begins prematurely and the nut dries too rapidly, the hull may close tightly on the shell, becoming difficult to remove. In California, the pattern of maturation across the range of almond genotypes extends from early August to late October. Following hull-split, the almond hull and kernel rapidly desiccate to below 7% moisture where mold development is effectively suppressed.

2.4 Tree Characteristics

Trees vary in size, shape, vigor, branching pattern, growth, and bearing habit. Characteristic patterns distinguish cultivars (Brooks and Olmo 1997; Gulcan 1985). These traits affect productivity, training and pruning needs, and adaptability to harvesting operations. Tree size is a relative term that depends not only on the individual genotype but also on orchard age, site (climate, soil), and management (irrigation, fertilization, and pruning). Size is related to precociousness and productivity. Some cultivars such as 'Merced' show reduced growth with age, partly as a consequence of precocious production, while others such as 'Nonpareil' tend to maintain vigor, resulting in larger trees. Size of an individual tree is directly correlated to yield and must be balanced against tree spacing and density to optimize production per hectare. Size of a tree also directly affects management efficiency, depending on the type of cultural system utilized. For mechanized harvest, fewer trees per unit are desirable. If trees are too large, however, they become difficult to shake, prune, and spray. Most cultivated almonds fall within the tree size range of medium to large, depending upon age and site.

Almond, as in all *Prunus*, initiates flower buds laterally on current season growth, which then bloom and fruit the following year (Fig. 2). In general, there are three basic classes of bearing habits: most flower buds on 1-year-old shoots as in 'Ai', most flowers on spurs as in 'Tuono', and mixed as in 'Mission' and 'Nonpareil'. A mixture of both bearing habits is considered advantageous. Shoot bearing habits are associated with precocious production, while spur habit greatly increases the bearing surface. Foliage density is, in turn, determined by the branching habit and the size and distribution of leaves. Foliage density differences can be visually characterized among cultivars. However, leaf size varies with position, with shoot leaves tending to be large and spur leaves small. A classification of growth habits based on variations in primary, secondary, and tertiary shoot development has been described by Gradziel et al. (2002a) and Kester and Gradziel (1990).

2.5 Fruit, Shell, and Kernel Characteristics

Almond fruits of different cultivars vary in size, shape, pubescence, shape and retention of the pistil remnants, and nature of the suture line (Monastra et al. 1982). In 'Drake', the suture line shows a relatively deep depression, while 'Nonpareil' has a relatively smooth line and 'Mission' fruit shows two prominent vertical ridges. The pattern by which 'splitting' occurs in the hull also differs and can be representative of cultivars. Four basic types have been described: ventral split opening on one side ('Peerless'), ventral and dorsal split ('IXL'), four-way split ('California'), and dorsal split ('Jeffries').

The thickness and weight of the mature hull may differ significantly among cultivars. Some hulls such as with 'Mission' are thin and dry and contribute only a small portion of the entire fruit. Others, such as 'Nonpareil', are thick and fleshy and provide a relatively large proportion of the weight. In California, hulls are used for livestock feed and the food value is better with larger hulls. Hull characteristics also affect the relative ease with which nuts are removed from the tree at harvest, the ability of nuts to dry rapidly during harvest, and the ease of hull removal. These processes are more critical with soft-shelled cultivars used in California where worm infestations and concealed damage from wet field conditions can be serious problems.

Shell hardness is associated with the total amount of lignin deposited to the shell during nut development. Shelling proportion (dry weight of kernel/dry weight of in-shell nut) is used to obtain a quantitative measure of shell density and is utilized in commercial activities to calculate kernel yield of different cultivars. Markings on the outer shell are characteristic of individual cultivars as well as different almond species. Within *P. dulcis*, the markings or pores tend to be mostly circular, less frequently elongated, and occasionally a mixture of both. Pores may be large or small, many or few. Other species have smooth and thin shells as with *P. bucharica* or are distinctly grooved or scribed as with *P. kuramica, P. tangutika,* and *P. persica.*

The integrity of the shell, particularly at the suture, is important since poorly sealed shells have kernels exposed and so susceptible to disease and worm damage. The shell consists of an outer and an inner layer separated by channels through which vascular fibers develop. As the hull dehisces and separates from the nut, the outer shell layer may remain attached to the hull and separate from the inner shell layer. The latter type is often associated with high shelling percentages and poor shell seal.

The almond has a large nonendospermic seed having two large cotyledons. Kernel size, shape, and weight are frequently related within cultivars (Arteaga and Socias i Company 2002). Kernel size is often expressed by linear dimensions of length, width, and thickness. These parameters are established during the first growth phase of nut development in the spring and are completed by early summer. Crop density is inversely related to average kernel size. Among kernels

of a given cultivar, a high correlation also exists between dry weight and linear dimensions of length and width. Average kernel weight is an important parameter of yield. Weight increases continuously until maturity. Improper filling may be caused by adverse growing conditions, moisture stress, early ripening, or other environmental and cultural stresses. Shape is a function of relationships among length, width, and thickness. The unique shapes of certain cultivars tend to establish specific marketing categories and uses. Irregularities in width and thickness may change the visual effect significantly. A high correlation was found to exist between width and length among kernels of the same cultivar even when compared in different years and from different locations (Kester and Gradziel 1996). The correlation between thickness and either width or length, however, was much less. As size dimensions decrease, thickness is not necessarily related. Consequently, the relative width to length may appear different for different genotypes otherwise having a similar kernel mass. Shape is usually described from a top view of the wider side of the kernel. Kernels may be round, oval, ovate, oblong, or straight when viewed on one edge, and rounded to various degrees on the other. Thickness (viewed from the edge) may vary from base to tip. Unequal thickness can result in unequal roasting during processing.

3 Breeding

Almonds, either in cultivated orchards or as feral or wild seedlings, have been an important source of food for thousands of years. Within each region, the best wild seedlings were routinely selected for propagation by local farmers, while natural selection continued its unrelenting pressures toward greater adaptation to local environments, including regionally important disease and insect pests. The self-sterile nature of almond insured a continuous exchange and mixing among cultivated and wild germplasm including, in many cases, related species (Grasselly 1972; Socias i Company 2002). Since wild almonds are also harvested for food in these areas, superior genotypes would be identified and propagated. Most modern cultivars in Asia, the Mediterranean area, and more recently in California originated as such time-tested seedlings selections. The subsequent selection over hundreds of years and hundreds of thousands of clonal propagations has also identified improved clonal sources for many of these well-established cultivars. Both genetic (deletions, point mutations, etc.), aneuploidy (see Martínez-Gómez and Gradziel 2003), chromosomal (translocation, see Jáuregui et al. 2001), and epigenetic (gene activation/silencing, etc.) changes would be selected, though because the subsequent selections are vegetatively propagated, the specific nature of inheritance is rarely analyzed.

In the early 1900 s, formal plant breeding programs were established in most major production areas to accelerate this selective process through controlled crosses and related genetic manipulations. While many goals such as total yield

and production efficiency were similar among programs, regional breeding goals often varied due to different environments, disease, and pest problems. At the same time, the globalization of the almond market imposed more stringent limits on acceptable kernel and shell characteristics. Despite inherent obstacles to rapid genetic improvement, including large plant size and the long seed-to-seed generation period of 4 years or more, many commercially successful cultivars have resulted from such controlled crossing programs in the last decades. Examples include the cultivars Ferragnes, Ferraduel, and Ferrastar from France; Butte, Ruby, Sonora, Padre, and Winters from California; and Guara from Spain. Regional almond breeding programs and their primary objectives have been reviewed by Kester et al. (1996).

3.1 Genetic Resources

Cultivated almonds show high levels of genetic variability because their self-sterility makes them obligate outcrossers and possibly due to their interspecies origin. Commercial cultivars within individual production areas, however, often show a limited genetic base due to their origin from only a few founder genotypes selected for their desirable regional value (Felipe and Socias i Company 1992). For example, most commercially important California cultivars originated from crosses between only two parents: 'Nonpareil' and 'Mission' (Bartolozzi et al. 1998; Hauagge et al. 1987; Kester and Gradziel 1996). Greater genetic variability and so increased breeding options for desired traits such as disease resistance are being pursued through the incorporation of breeding material from other regions (Kester and Gradziel 1996; Martínez-Gómez et al. 2003; Socias i Company 1998). Because of the probable interspecies origin of many of these cultivars (Kester et al. 1991; Ladizinsky 1999; Socias i Company 2002), improvement of specific genetic traits may also benefit from the introduction of genes directly from related species. Hybridization between *P. dulcis* and other almond species has often taken place naturally wherever different species come into contact. *P. webbii* grows throughout the Mediterranean region and its range intersects with cultivated almond in Italy Sicily, Spain, and Greece. Hybridization has occurred and introgression evidently results. In the Apulia region of Italia, *P. webbii* has been found to be the source of self-fertility (Godini 2002). The range of almond species is extensive with a wide diversity of traits (Gradziel et al. 2001a; Kester and Gradziel 1996). Controlled crosses of *P. dulcis* with other almond species in sections *Euamygdalus* and *Spartiodes* have been readily carried out (Gradziel et al. 2001a; Gradziel 2003). Hybridization with section *Lycioides* is possible though somewhat more difficult and even more difficult with *Chamaeamygdalus*. Despite their physical and developmental differences, crosses with peach (*P. persica, P. mira*, *and P. davidiana*) can be readily achieved and have proven to be particularly valuable

as rootstocks as well as sources of commercially useful traits (Gradziel et al. 2001a; Gradziel 2003).

3.2 Objectives and Approaches

The goal of cultivar improvement programs is the development of improved cultivars highly adapted to local environments and market demands. Since both market requirements and local adaptation placed considerable limits on the final genetic makeup, most breeding programs pursue the incremental improvement of locally established varieties, typically by the sequential addition of new genetic value (disease resistance, nut quality, maturity time, productivity, etc.). Basic objectives of most almond breeding programs target increased yields, improved quality, and decreased production costs (Socias i Company 1998). These traits have been found to be largely inherited in a quantitative manner (Kester et al. 1977; Spiegel-Roy and Kochba 1981) with a few exceptions such as self-compatibility and kernel bitterness. Heritabilities for important breeding traits have recently been reviewed by Kester et al. (1996), Dicenta et al. (1993a, b), and Socias i Company et al. (2007).

A classical breeding approach toward these goals would involve an initial hybridization between selected parents, followed by introgression of the traits of interest, typically by backcrossing to the parent with the most promising commercial potential. While new genetic engineering techniques offer significant advantages for the discrete addition of new genes to commercially established cultivars, the current dearth of transgenes useful to tree crop breeding limits its present application. Other new biotechnology approaches, particularly gene mapping and gene tagging, offer the promise of greater efficiencies in the areas of gene discovery and gene and introgression (Martínez-Gómez et al. 2006). In addition, the probable interspecies origin of many modern almond cultivars suggests promising opportunities for the manipulation of not only the traditional genetic (i.e., Mendelian) determinants but also the epigenetic controls, which are only recently becoming characterized. Epigenetic modification may have particular value for almonds breeding because epigenetic variability appears to be greatly enhanced with interspecies hybrids (Grant-Downton and Dickinson 2006) and commercially valuable epigenetic variants can be effectively captured in cultivars by the vegetative propagation common in tree crop cultivar dissemination (see Kester et al. 2004).

Epigenetic-like changes (i.e., brought about by an apparent change in gene activity rather than gene DNA sequence) have been documented in clonal differences within cultivars and in a more fully characterized epigenetic disorder known as ‘noninfectious bud failure’. Noninfectious bud failure, which threatens over 50% of California production, is expressed as a deterioration of the clone vitality with increasing age, leading to bud failure in individual trees and

branches. Initial symptoms include the necrosis of the growing point of vegetative buds during the fall. The resulting shoot phenotype, as expressed the following spring, is a failure of terminal and/or subterminal vegetative buds to grow. If the terminal bud fails, 'dieback' results. However, lower and later developing buds may survive providing a 'flush' of new growth at basal and subterminal sites of the shoot. 'Rough-bark' areas sometimes develop in narrow bands on the shoots. New shoots from surviving buds grow vigorously and, when this sequence is repeated in consecutive years, result in an erratic growth pattern, often referred to as 'crazy-top'. Kester et al. (2004) have recently shown that control of this type of epigenetic disorder can be achieved through well-designed certification programs similar to those used to control vegetatively propagated viruses. Such programs have three basic steps: identification of single tree sources which test negatively for the disorder in clonal-source screening trials (see Kester et al. 2004); maintenance and registration of a limited number of trees of the selected clone-source in a foundation orchard; and limited multiplication of registered material to provide certified trees for commercial nurseries (Uyemoto and Scott 1992).

Because epigenetic changes do not respond to traditional breeding methods designed to manipulate classic Mendelian genes, they are generally perceived as undesirable and routinely rouged out using hybridization strategies or for vegetatively propagated crops, clonal selection strategies as described above. However, as both genetic and epigenetic compositions can be captured through clonal propagation, the same methods used to rogue out epigenetic changes can also be utilized to capture desirable epigenetic arrangements. An example would be the widespread practice among nurseries in selecting superior clonal sources of important vegetatively propagated cultivars (Hartman et al. 2002). Epigenetic capture offers unique advantages to breeding programs utilizing wide crosses, since the interspecific hybridization process has been shown to increase the levels of epigenetic variability resulting in novel and transgressive phenotypes (where the trait is expressed at levels beyond the sum of the parents). This breeding approach has recently shown success for peach cultivar improvement where advanced processing peach selections derived from almond–peach interspecific hybridization expressed fruit ripening patterns not evident in either species parent (Gradziel 2003). Regardless of approach, almond breeding objectives typically fall in three general areas: increase yield, improve market quality, and decrease production costs.

3.3 Self-Fruitfulness

Insufficient cross-pollination is frequently the major determinant of commercial yield in self-sterile almond (Asai et al. 1996; Micke 1994). Self-fruitfulness results from the combination of self-compatibility (i.e., self-pollen shows compatible growth to fertilization on pistils of its own flower) and autogamy (i.e., a

flower structure promoting consistent self-pollination). Autogamy appears to be controlled by a number of genes (Kester et al. 1996) affecting flower structure as well as the more dynamic aspects of the flowering process including timing of answer dehiscence (Gradziel and Weinbaum 1999) and pattern of stigma growth relative to maturing anthers (Godini 2002). Although highly autogamous selections have been identified, the genetic manipulation of this trait remains uncertain. Self-compatibility, as with self-incompatibility, is controlled by a major gene (Dicenta and García 1993b), though modifier genes also play important roles (Gradziel et al. 2002b). While many almond species demonstrate some level of self-compatibility, in a cultivated almond background only the self-compatible genes from *P. mira, P. persica,* and *P. webbii* resulted in fruit set above the 30% considered desirable for commercial production (Gradziel 2003a, b). Breeding populations developed from interspecies crosses segregate for self-compatibility in the expected Mendelian ratios for a single gene (Dicenta and García 1993a; Gradziel et al. 2001b; Socias i Company and Felipe 1988, 1992). *P. mira*, the species-cross showing the highest selfing percentages following introgression of the self-compatibility gene, also showed high levels of self-pollination (Gradziel et al. 2001). Long-term efforts to breed self-compatible almonds have been reviewed by Socias i Company (1990).

3.4 Diseases

The most serious foliage diseases of almond include shot hole caused by *Stigmina carpophila* (syn. *Coryneum beijerinkii*), travelure *(Fusicladium amygdali)*, polystigma (*P. occhraceum*), fusiccocum (*Fusicocum amygdali*), and anthracnose (*Gloeosporium amygdalinum* and *Colletotrichum acutatum*). Relative susceptibilities of important cultivars in different countries have been determined and potential sources of resistance have been identified (Kester et al. 1991).

Blossom and twig blight, the major crop-limiting fungal disease worldwide, is caused by (*Monilinia laxa* and *M. cinerea*). These fungi attack the flowers and are most serious in years when rain occurs with bloom. Other fungi, including *Botrytis cinerea*, can also be a serious problem under these conditions. Aflatoxin producing *Aspergillus flavus* infections of the kernel is a major problem, particularly where insect damage is common (Dicenta et al. 2003; Gradziel and Kester 1994; Gradziel et al. 2000; Gradziel and Wang 1994). Although disease control has been possible through fungicides, the need to consider natural resistance becomes more important with the continued loss of agrochemicals.

Almonds can be infected by the same range of viruses as other *Prunus* including the ALAR viruses (ringspot, prune dwarf, line pattern, calico, and apple mosaic) and NEPO viruses (tomato black ring, tomato ring spot, and yellow bud mosaic). Leaf and flower mosaic phenotypes can result from the combination of several viruses. Several complexes of virus-like disorders that

produce 'stem pitting' and 'graft union brown line' are known but not well understood (Uyemoto and Scott 1992). However, many cultivars of almond appear to be immune to the plum pox virus, which remains a serious problem for most stone fruits (Martínez-Gómez et al. 2004).

3.5 Pests

In California, navel orangeworm (*Paramyelois transitella*) and peach tree borer (*Anarsia lineata*) can cause serious damage to nuts at harvest (Rice et al. 1996). This problem is related to the vulnerability of soft, paper-shell, and poorly sealed sutures common to California cultivars, including 'Nonpareil', 'Ne Plus Ultra', and 'Merced' (Gradziel and Martínez-Gómez 2002). Partial control is achieved by integrated pest management, particularly orchard sanitation (IPM Manual Group of U.C. Davis 1985). Resistance through better-sealed shells has been observed in some cultivars including 'Carmel', 'Mission', and 'Butte'. This problem is not serious in the Mediterranean area because of the characteristic well-sealed, very hard, and thick shells of the major cultivars.

Mite species, including pacific spider mite (*Tetranychus pacificus*), two-spotted spider mite (*T. urticae* Koch), European red mite (*Pannonycus ulmi* K), and brown almond mite (*Bryobia rubriculus* Scheuten), can adversely affect production and may be locally important, particularly in conditions of moisture stress. Variation in susceptibility exists among different cultivars.

The almond wasp (*Eurytoma amygdali* End) is an important pest from the Middle East extending into Greece. It attacks the young developing nut. Other significant Mediterranean pests that attack the trunk and branches of trees include *Scolytus amygdali* Guerin and *Capnodis tenebrionis* L. C*apnodis*, a species of borer that attacks the trunk of trees in the Mediterranean basin, particularly trees that are under stress.

3.6 Rootstock Diseases

Crown gall (*Agrobacterium tumefaciens*) can infect the root and crown of nursery trees through previous injuries and then remain with the tree in the orchard where it can cause serious losses (Kester and Grasselly 1987). Peach, almond, and the peach–almond hybrids are susceptible. Oak root or honey fungus (*Armillaria mellea*) is another root fungus of worldwide distribution. Greater tolerance of this problem has been reported in certain plum species but no actual resistance has been described. 'Crown rot', 'wet feet', and 'water-logging' are names given to conditions resulting in deaths of trees associated with excess moisture over a period of time. These conditions have been related to asphyxia and to attacks by various *Phytophthora* species. The symptoms

include dieback at the crown or at smaller roots, depending upon the fungus species, time of year, temperature, and moisture conditions in the soil. Almond, peach, and peach–almond hybrids are generally susceptible, with variation present among species. Plum rootstocks have a higher level of resistance and are the primary rootstocks planted under high soil moisture conditions.

Soil-borne nematodes are problems for almond and peach in many parts of the world (McHenry and Kretsch 1987). Important species affecting almond include root knot (*Meloidygyne incognita* and *M. javanica*), ring nematode (*Criconemoides* spp.), dagger nematode (*Xiphinema* spp.), and lesion nematode (*Pratylenchus* spp.). Dagger nematode is a vector for several viruses, including tomato ringspot virus, which causes 'brown line' in almond, and yellow bud mosaic. Ring nematodes are associated with predisposition of young almond trees to bacterial canker. Root knot nematodes are common in warmer parts of the world with sandy soil. Sources of resistance to *M. incognita* were discovered in certain peach selections including 'Shalil', 'Yunnan', and 'Bokhara' from China and in some almond selections from Israel. Root knot nematodes were later found to have an additional species (*M. javanica*), and a source of resistance was discovered in the wild peach *P. davidiana*.

4 Root Stock Improvement

Almond seedlings have been the traditional almond rootstock used under non-irrigated and well-drained soil conditions. Advantages include easy propagation from seed, excellent compatibility with almond cultivars, deep rooting ability, and high tolerance to drought and calcareous soils. However, almond rootstocks perform poorly on excessively wet soils during active growth. Almond seedling rootstocks are also susceptible to important disease and nematode problems including crown rot (*Phytophthora* spp.), crown gall (*A. tumefaciens*), oak root fungus (*Armillaria* spp.), and root knot, ring, lesion, and dagger nematodes. Because almond rootstocks are very susceptible to fungal diseases and asphyxiation in wet and poorly drained soils, almond cultivars under irrigation are usually planted on three general classes of rootstock: peach, plum, or almond–peach hybrids (Barbera et al. 1994; Rom and Carlson 1985).

4.1 Peach

Almond trees on peach rootstocks grow more vigorously when young, come into bearing somewhat sooner, and tend to survive better than comparable trees on almond rootstocks. The reason for greater tree survival may be a greater tolerance to higher soil water contents, crown rot, and crown gall. Peach is not tolerant of soils that are calcareous, subject to drought, or high in boron. Trees

on peach rootstock are not considered as long-lived as those on almond, but this factor may vary with site conditions, management, and cultivar. 'Lovell' peach seedlings have been the main peach rootstock used in California, though other peach cultivars such as 'Halford' have been substituted with about equal results. With the entry of nematode-resistant or -immune sources, such as 'Nemaguard', a shift has been made to seedlings of nematode-resistant rootstocks in more sandy soils where nematode damage is a problem.

4.2 Plum

Plum species are in a different taxonomic section of *Prunus* than almond and peach and may exhibit incompatibility when used as a rootstock for some almond cultivars (Kester 1970). Almond cultivars may be grafted to certain plum species including *P. cerasifera, P. salicina,* and *P. domestica*. Other plum species rootstocks may survive and grow for long periods but do not provide adequate yield and performance to become a standard commercial rootstock; but they may be potential sources of genes useful for rootstock breeding. Interspecific hybrids between plum and almond, peach, or other plum species have been developed. Important traits possessed by plums include ease of vegetative propagation, resistance to high soil moisture, nematodes, and some diseases such as oak root fungus. The most significant commercial plum rootstocks for almond are the 'Marianna' hybrids—a group of clones arising from a breeding line believed to be *Prunus myrobalan* × *P. hortulana*. Of this group, 'Marianna 2624' is an important rootstock for almond in California for use in finely textured soils with poor drainage and where oak root fungus has occurred. 'Marianna 2624' is also nematode-resistant. Some almond cultivars including the major cultivar 'Nonpareil' can be incompatible on 'Marianna 2624' and related clones, however.

4.3 Almonds × Peach Hybrids

Almonds–peach hybrids generally show strong hybrid vigor and high uniformity. Morphologically, hybrids are intermediate between the parents, and various traits can be exchanged readily between the two species. Particularly useful traits include vigor, nematode resistance, tolerance to replant situations and calcareous soils, and a deep, well-anchored root system. While shoot tip culture can be used to propagate almond–peach hybrid clones, such as 'GF 677' in Europe and 'Hansen' in California, hardwood cuttings provide the most economical nursery clonal propagation method, provided sufficient rooting percentages are obtained. Leafy cuttings (leaf-bud, softwood, or semi-hardwood) under mist or in enclosures can increase the probability of rooting but require higher costs and special facilities.

Micropropagation can increase the range of genotypes propagated, but it also increases the cost of nursery propagation. At the same time, micropropagation has shown promise for the direct rooting of scion material and difficult-to-root rootstock clones and for the rapid increase of new or virus-free cultivars. Explant sources utilized for culture include shoots, leaf petioles, and seed. When endocontamination is a problem, as in long shoot tips and sections of stem pieces, surface-sterilized explants are first placed in a pretreatment medium for 2 or more weeks to allow contaminated material to be identified (Tabachnik and Kester 1977). Scales can also be removed from buds to expose the growing tip, which is then excised and cultured on an appropriate media for elongation and proliferation of lateral buds. The vegetative propagation of almond clones, either as rootstocks or as own-rooted plants, is generally difficult. Shoots of 'Nonpareil' have been established in culture, but rooting and long-term maintenance are difficult.

4.4 Rootstock to Scion Compatibility

The most compatible scion/rootstock combinations are almond–almond. Almond–peach combinations are almost as compatible except that a peach overgrowth generally appears at the union, which can vary by cultivar. No adverse effect has been reported, although some cases of a 'brown line' at the union of 'Milow' almond/'Lovell' peach has been observed. Almond/(peach–almond hybrid) combinations also have smooth unions. Graft combinations of almond–plum and plum hybrids produce varying degrees of incompatibility symptoms (Kester et al. 1965). Graft union abnormalities may occur that cause strong overgrowths or disturbances at the union. This disfunction on 'Marianna 2624' generally occurs only in the bark and not in the sapwood. Symptoms are primarily expressed as disturbance of the normal annual growth patterns, with premature foliage yellowing, and early abscission in late summer and fall. Reduced shoot extension, sparse foliage development, shoot dieback, reduced tree size, excessive spur production, and severe overgrowth tend to follow.

5 Biotechnology

The recent development of powerful new biotechnologies has advanced plant-breeding efforts through the direct incorporation of foreign genes using genetic engineering strategies and through the ability to use a DNA molecule directly as markers for desired traits. While almond cultivars are readily transformed using Agrobacterium-mediated approaches, the regeneration of plantlets from established cultivar cells has proven very difficult. This difficulty is believed to be due to the recalcitrance of cultivar cells to initiate the required organogenesis, presumably because they have lost their juvenility with their advanced clonal age. Molecular markers, however, promise to dramatically increase breeding efficiency as

they offer the opportunity for fast, accurate, and environment-independent evaluation at the seedling stage. In addition, specific markers offer the advantage of codominant expression, good reproducibility, and allow the ability to compare genetic variation among homologous regions of the same or different species (Martínez-Gómez et al. 2003). A detailed review of biotechnology research with almond has recently been provided by Martínez-Gómez et al. (2006).

5.1 Molecular Markers

The most important molecular markers used in almond studies are isozymes, restriction fragment length polymorphisms (RFLPs), randomly amplified polymorphic DNAs (RAPDs), simple sequence repeats (SSRs), and markers based on unique DNA sequences. Isozymes were one of the first molecular marker evaluations available to almond studies and offered codominant expression and good reproducibility, but were limited by the small number of loci that could be analyzed by conventional staining methods, as well as a low genetic variation at most loci. Nonetheless, it was isozymes studies which first documented extensive genetic variability in almonds overall, as well as the limited genetic base of many almond-breeding programs (Arulsekar et al. 1989; Hauagge et al. 1987; Vezvaei et al. 1995). RFLPs are also codominant but can detect a virtually unlimited number of markers. In almond, RFLPs have been used for discovering linkages between markers, for constructing genetic maps, for cultivar identification, and for the characterization of genetic variability. RAPDs based on PCR amplification of arbitrary primers have been useful for characterizing germplasm variability (Bartolozzi et al. 1998; Martins et al. 2003), but had limited application for cultivar identification and map construction since they are dominant markers with occasional difficulties with repeatability. SSR or microsatellite markers, which are also based on PCR amplification, have proven more useful for genetic relationships (Martínez-Gómez et al. 2003a), cultivar identification (Martínez-Gómez et al. 2003b; Martins et al. 2003), and map construction (Dirlewanger et al. 2004) due to their high polymorphism, codominant inheritance, abundance, and the frequent successful amplification of SSR markers developed in related species (Martínez-Gómez et al. 2006).

5.2 Genetic Linkage Maps

SSR analysis confirmed previous isozymes studies which identified the almond as the most polymorphic species within the major *Prunus* tree crop species (Martínez-Gómez et al. 2006) making it an ideal candidate for map construction. Extensive research, particularly in Europe (see Ballester et al. 1998; Ballester et al. 2001; Corredor et al. 2004; Dirlewanger et al. 2004; Martínez-Gómez et al. 2006), led to the development of a high-density almond map,

which includes 562 markers (361 RFLPs, 185 SSRs, 11 isozymes, and 5 STSs) covering a total distance of 519 cM with an average density of 0.92 cM/marker and largest gap of 7 cM (Dirlewanger et al. 2004). The order of molecular markers observed in the almond map was similar to maps developed with other *Prunus* species suggesting a high level of synteny within the genus (Dirlewanger et al. 2004; Martínez-Gómez et al. 2006). This homology among *Prunus* genomes supports the opportunity for successful interspecific gene introgression as demonstrated by the successful transfer of traits from closely related species to almond (Gradziel et al. 2001a; Martínez-Gómez et al. 2003b). The high level of synteny within the genus also supports the transferability of genetic information developed from linkage maps of other *Prunus* species.

5.3 Trait Mapping and Gene Cloning

The availability of high-density linkage maps has allowed recent successes in establishing the approximate map position of major genes in almond. Important examples include the use of bulk segregant analysis (BSA) to map the self-incompatibility gene (Ballester et al. 1998), as well as a major gene controlling delayed flowering time (Ballester et al. 2001; Grasselly 1978; Socias i Company et al. 1999). Root-knot nematode resistance in an almond–peach hybrid has also recently been reported by Dirlewanger et al. (2004). In addition, the physical mapping of rDNA genes by Corredor et al. (2004) has allowed the establishment of a more precise karyotype for almond.

Cloning of genes expressed during seed development has been reported by García-Mas et al. (1996). Suelves and Puigdomenech (1998) have described the cloning of the mandelonitrile lyase gene responsible for the creation of both cyanide and the amaretto flavor of bitter almonds.

A major effort has been directed toward cloning and characterizing the economically important self-incompatibility gene in almond (Bacarella et al. 1991; Certal et al. 2002). The cDNA encoding almond S-RNase was first cloned by Ushijima et al. (1998). To better understand the nature of the self-incompatibility gene, Ushijima et al. (2001) later cloned and characterized the cDNA encoding mutated S-RNase from the almond cultivar 'Jeffries', which has a disfunctional S-allele haplotype in both pistil and pollen.

5.4 Marker-Assisted Selection

PCR-based markers of almond self-incompatibility S-alleles have been successfully used to identify different self-incompatibility genotypes (Barckley et al. 2006; Channuntapipat et al. 2003; Tamura et al. 2000). Similar results were obtained by Boškovic et al. (2003) who identified major almond cultivar stylar

S-RNase by electrophoresis in vertical polyacrylamide gels. PCR-based markers of almond self-incompatibility S-alleles have been employed to facilitate the integration of self-compatible S-alleles from related species (Gradziel et al. 2001a). Screening efficiency and flexibility has been greatly increased with the development of successful multiplex PCR techniques by Sánchez-Pérez et al. (2004). Using advanced cloning strategies, Ushijima et al. (2003) have recently described the structural and transcriptional analysis of a pollen-expressed F-box gene with haplotype-specific polymorphism strongly associated with self-incompatibility.

Molecular markers are currently being employed to elucidate the genetic basis of plant processes controlled by multiple genes. For example, Campalans et al. (2001) have described a differential expression technique based on cDNA-AFLP (amplified restriction fragment polymorphism derived technique for RNA fingerprinting) to characterize genes involved in drought tolerance in almond. Results identified increased drought tolerance in specific genes associated with leaf function.

Despite these recent advances in the application of the newer biotechnologies, almond, as well as other tree crops, lags behind the progress typically observed for annual crops. This is, in large part, the consequence of the inherent difficulties in doing genetic studies on such large-sized and long generation-time plants (Martínez-Gómez et al. 2003). However, these inherent obstacles to traditional breeding make the opportunities with the new technologies much more revolutionary when applied to tree crops. When fully integrated with the array of breeding methods developed to capitalize on the inherent advantages of tree crops, such as the capability to capture desirable genetic/epigenetic arrangements through vegetative propagation, breeding potential could be expected to surpass that for seed-propagated annual crops. Almond is currently well positioned to be a leader in this effort.

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