

Review Article

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Genetic Analysis of Almonds (*Amygdalus*) *in Silico*

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Nut trees and shrubs of perennial and outcrossing sweet almond (*Amygdalus dulcis*: 2n=2x=16) grown on temperate zone belongs to the plant clade Rosids, order Rosales, family Rosaceae (Syn.: *Amygdalus communis*, *Amygdalus dulcis*, *Prunus amygdalus*, and *Prunus dulcis*) [Bauhin, C., 1623; Ray, J. 1686; Linné, C., 1753; Soó, R. and Jávorka, S., 1951] [1-3].

Rosaceae comprises >95 genera and >3.000 species, half of these >1.500 are woody species with numerous fruit trees grown in Northern temperate zone [4].

Most of the genome-, nuclear-, cp-, and mtDNA sequences analyzed here clustered almond into individual cluster indicating the use of genus name *Amygdalus* rather *Prunus*. Here, the new results of almond genetics are reviewed and discussed.

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Received: August 15, 2026; **Accepted:** August 21, 2026; **Published:** September 10, 2026***Almond (Amygdalus Dulcis)***

Species of *Rosaceae* family are divided into four subfamilies based on fruit type morphology of *Amygdaloideae* (with stone fruits), *Maloideae* (with pome fruits), *Rosoideae*, and the dry fruited *Spiraeoideae* according to the classical systematic in [5]. The genus *Amygdalus* comprises >25-26 species and includes wild species, and the cultivated sweet almond (*A. dulcis*), bitter almond (*A. amara*) (due to benzaldehyde and hydrocyanic acid content), small almond shrub (*A. nana*), and dwarf and bonsai almonds [6,7].

Special varieties of sweet almond has thin ('paper') shell, e.g., the cv. 'Nonpareil' (meaning 'having no equal') grown in California where 80% of the world yield is produced. Sweet almond is cultivated for edible nuts, whilst bitter almond is used for human tumor therapy and beverage industry (e.g., 'Amaretto').

A. fenzliana growing in the mountainous Caucasus region, *A. kuramica* and *A. scoparia* are assumed to be the ancestral species of cultivated almond [9,10].

The ancestral species of *Prunus* (*Amygdalus*) *arabica* (<https://grinczech.carc.cz>) was also used recently in almond breeding [11].

Archaeobotany of Almond

- 11,000 BC. The oldest almond seed remains together with pistachio were excavated from Franchthi Cave (Greece)

collected there by birds, rodents or man [11].

- 1,400 BC. In the Bible's Book of Numbers Aaron's almond rod blossomed and bore almonds.
- 1,332-1,323 BC. Tomb of Tutankhamun revealed almond seeds [12].
- 600-900 AD. Almond reached the Roman Empire and Europe from Asia through the Silk Road trade route (In: Stein, 1932; <https://www.himalayanclub.org>).
- 1,700s AD. From Europe almond reached California (USA) by European padres.

In Europe, after the invasion of American aphid (*Phylloxera vitifoliae*) to grape (*Vitis vinifera*) the whole European viticulture and viniculture (1863-1885) were devastated and moving towards East reached Hungary (1875-1914) [13].

Large almond plantations were developed on the former grape fields (e.g., Budatétény and north border regions of Lake Balaton), organized by Miklós, G. [1832-1894], Ministry of Agriculture, Budapest, Hungary.

Sweet almond cultivars were collected worldwide started with Yalta collection (Nikita Botanical Gardens, Russia/Ukraine), 1935 [14,15]. (Figures 1, 2).



Figure 1: Huge Collection of Native Sweet Almond Nuts (*Amygdalus dulcis*) (1-49) From Uzbekistan, Collected in 2010 (Photo by Molnar, T.) (Reedited Figure of [14].



Figure 2: Registered Sweet Almond (*Amygdalus dulcis*) Cultivars from the Collection of Nikita Botanical Gardens, Yalta (Reedited Figure of [14].

Almond and Related Species

Diploid and polyploid almonds had developed during evolutionary speciation [18,19].

Eg, next to the diploid ($2n=2x=16$) species of *A. dulcis* (sweet almond), *A. mongolica* (Mongolic almond), *A. tangutica* (Tangut almond), *A. tenella* (wild almond), and polyploids of *A. triloba* (ornamental almond) ($2n=8x=64$) and *A. pedunculata* ($2n=12x=96$) (long stalk almond) have developed www.efloras.org [20,21].

Based on early morphological comparisons (Darwin, 1869; In:[22] based on flowers, leaf shape and sizes, almond probably has the closest similarity to domesticated peach (*Prunus persica*) without flashy mesocarp. Genome sequences showed high similarity with only a mean of 20 nucleotide substitutions per kbDNA. The sequence analysis showed 5.88 MY for the divergence between peach and almond [22].

Wild ancestors of domesticated peach *P. davidiana*, nectarines (*P. persica* var. *nucipersica*), and the Chinese flat peach also show high level of morphological diversity [23]. Surfaces of nuts (i.e., shells) [24] are different in almonds and peaches (1, 2, 4). Nevertheless, seeds of peaches have the same bitter or sweet taste like bitter almond due probably to amygdalin content (personal observation). Among apricots (*P. armeniaca*) there are also sweet and bitter seeded cultivars.

Bitter Almond vs Sweet Almond

The cytochrome P450 monooxygenase enzymes family (CYP79 and CYP71) of PdCYP79D16 (NCBI# MH992767.1; 1,605 nt mRNA) and PdCYP71AN24 (NCBI# MK014211.1; 1,561 nt mRNA) genes regulate seed taste of almond [25] (Figure 3/a).

Plant breeders use gene cluster symbols of homozygote dominant SK of sweet seeded almond, which is dominant over homozygote recessive sk gene of bitter almond [26].

Through crossing, three genotypes develop, the homozygote dominant diploid Sk/Sk (with sweet seeds), homozygote recessive sk/sk (with bitter seeds) and the heterozygote Sk/sk (with sweet or semi bitter seeds) (Almond Board of California; www.almonds.org).

In human digestion, amygdalin releases toxic hydrogen cyanide. The reaction is catalyzed by the beta-glucosidase enzyme (EC:3.2.1.21) which hydrolyzes amygdalin to prunasin and mandelonitrile (Figure 3/b).

Almond Growing Areas

Computer simulation of six almond species was exposed to 29 environmental and climatic factors including global warming [21-29]. The study indicated that areas of *A. dulcis*, *A. mongolica*, and *A. tenella* tend to expand to northwest; the areas of *A. tangutica* and *A. pedunculata* expand towards northeast and *A. triloba* to southwest [30].

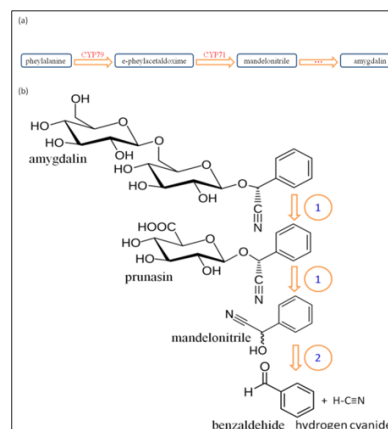


Figure 3: (a) The First STEPS of Biosynthesis of the Amygdalin Glycoside from Phenylalanine Amino acid Catalyzed by CYP79 and CYP71 Enzymes. (b) Enzymatic Break Down of Amygdalin Glucoside in Bitter Almond (*Amygdalus Aamara*). The #1 Indicate Beta Glucosidase Enzyme Acting in Two Steps (630 aa; UniProt #A0A5E4G187; EC:3.2.1.21; www.uniprot.org); Followed by #2 (S)-hydroxynitrile lyase (261 aa; UniProt #A0AAD4V6U1; EC:4.1.2.47; www.uniprot.org; www.enzyme-database.org) Which Releases Toxic Hydrogen Cyanide (Redrawn Figs. of [25,31]).

Grafted and Hybrid Almond Cultivars

Recent advances in almond breeding have yielded a series (>1400) of new almond clones and hybrids [9][26], e.g., *P. webbii* x [*Almond* cv. 'Nonpareil' x *P. persica*] (Figure4/1) and [*Almond* cv. 'Nonpareil' x *P. persica*] (Figure4/36). The *P. persica* x *P. davidiana* (the ancestor of peach), showed no hybrid vigor (Figure4/32) in seed/kernel mass (0.11 g - 2.08 g).

Interspecific F1 population was generated between sweet almond cv. 'Um el Fahem' x *Prunus arabica* a local wild almond species producing 92 hybrid seedlings, and the inheritance of six agriculturally important traits were analyzed [10].

The main Hungarian almond cultivars, e.g., 'Tétényi keményhéjú' [32] have different levels of frost tolerance and self-fertility [33]. In a preliminary field trial of ten Spanish cultivars, a non-self-fertile

and late flowering cv. ‘Marcona’ produced the highest yield in Hungary, 2026 (Dlusztus M, personal communication).

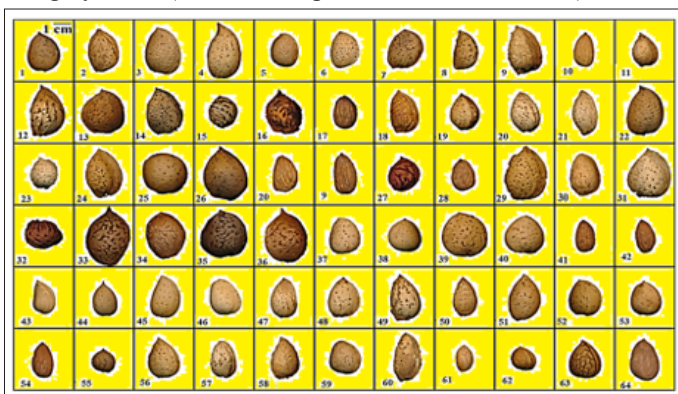


Figure 4: Samples of Sweet Almond (*Amygdalus dulcis*) Nuts Offspring of Introgressive and Interspecific Hybrids Reedited Figure of [9].

Bitter almond (*A. amara*) was also been found to be the best root stock for peaches (*P. persica*) by transmitting disease tolerance, e.g., leaf curls resistance (*Taphrina deformans*; Ascomycota) [34] and S. Gyulai’s (1923-2000) observations about 60 years ago, Budatétény, Hungary. Root stock of wild almond *Amygdalus/Prunus scoparia* (from Asia), is used to transmit drought resistance to sweet almond scion [8].

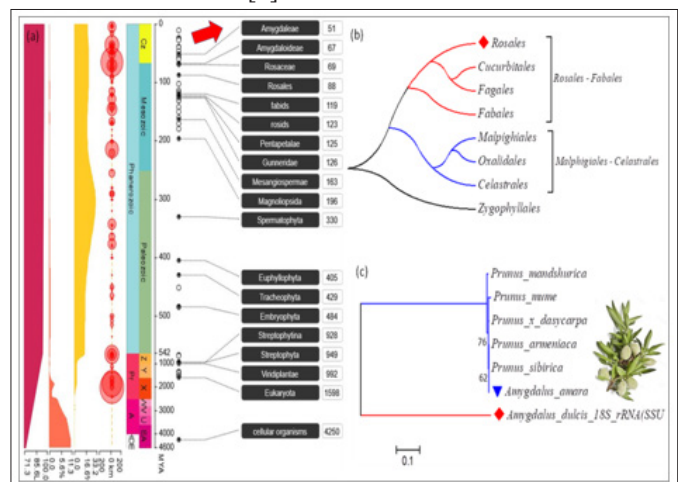


Figure 5: (a) Evolutionary Development of Almond (Genus *Amygdalus* of *Amygdaloideae*) (51-67 MYA) (Indicated by Arrow) Compared to the Development of Order Rosales (88 MYA) (TTLO5 Timetree.org [35]) (b) Phylogenetic Subtree of Order Rosales (based on data of TTLO5 timetree.org) With the Closest Orders of Rosales-Fabales (Neighbor Joining, NJ, phylogram edited by MEGA7 computer program [36]). (c) Molecular ML Phylogram (Maximum Likelihood) Of Gene Sequence of 18S RNA (SSU) to Compare *A. Dulcis* (SWEET ALMOND) to *A. Amara* (BITTER ALMOND) and Related Species of *Prunus* *mandshurica* (MANCHURIAN APRICOT), *P. Mume* (JAPANESE APRICOT / CHINESE PLUM), *P. Armeniaca* (APRICOT), and *P. Sibirica* (SIBERIAN APRICOT). Gene Sequences Were Downloaded From NCBI Server [37] aligned to *A. Dulcis* gene sequences (1,054 bpDNA; JN940934), cut to the Same Consensus Sequence Length (706 bpDNA) by ClustalW Computer Program [38] inbuilt to NCBI Server and by Bio Edit Computer Program [39].

Almond Evolution and Breeding

Sweet almond (*A. dulcis*) was found to be developing 51 MYA in our study.

Parallel evolution of almond species was assumed to occur between continents of Eurasia and North America concerning the native American species of *Prunus fasciculata* (desert almond), *P. fremontii* (desert apricot, harvested by Cahuilla Indians, one of the 52 Native American tribes), and *P. eremophila* (Mojave Desert plum, described recently, 2001) growing in the New World [21] (Figure 6c).

As with all Rosaceae fruit trees almond is easily infected by molds of *Monilia* [26], and aflatoxins producer *Aspergillus* [26] [13]. The ML Phylogram (Maximum Likelihood) was Edited by Computer Program MEGA7 With x1,000 Bootstrap Replication (unit 0.1 of Genetic Distance).

Almond Genomes

The sequenced haploid (n) genome of almond (*Amygdalus dulcis*, n=x=8) is 227.6 Mbp DNA, with gene numbers 26,936 (GCA_902201215.1) [29]. The size of cp (pltd) genome is 157.723 bpDNA (NC_034696), and the huge mtDNA genome is 444,092 bpDNA (CM038036.2) as in most plants [40].

To compare, the genome of *Arabidopsis thaliana* (Thale cress; n=x=5) is 119.1 Mbp DNA, gene# 38,312 (TAIR10.1), cpDNA is 154,478 bpDNA (NC_000932), and the mtDNA is 367,808 bpDNA (NC_037304).

Unlike genus *Amygdalus*, genus *Prunus* comprises high numbers of species (>300) (<https://powo.science.kew.org/>), including peache (*P. persica*), apricot (*P. armeniaca*), sweet- (*P. avium*) and sour- (*P. cerasus*) cherries, plum (*P. domestica*), myrabolan (*P. cerasifera*), blackthorn (*P. spinosa*), blackthorn x plum [prun plam], hackberry (*P. padus*), wild black cherry (*P. serotina*), cherry laurel (*P. laurocerasus*), and chokecherry (*P. virginiana*), (www.woodlandtrust.org.uk) [huckleberry belongs to *Vaccinium* genus of family Ericaceae].

Nuclear Genes

To estimate molecular distance between sweet almond and bitter almonds and related species the 18S nuclear ribosomal RNA (SSU, small subunit) gene sequences were compared by aligning to sequence of *A. dulcis* (NCBI #AF318754.1; 1,054 bp) (Figure 5/c).

The DNA sequence differences observed here indicated that *A. amara* differs from *A. dulcis* not only in the amygdalin producing genes, but also in other genes, e.g., diosgenin genes (PubChem CID 99474). These genes may arrange in a common gene cluster [31].

Chloroplast Genomes

Complete chloroplast genomes of almond [40] and related species were aligned to sweet almond (157,723 cpDNA; NC_034696). The phylogram (Figure 6a) showed almonds grouped in a distinct clade.

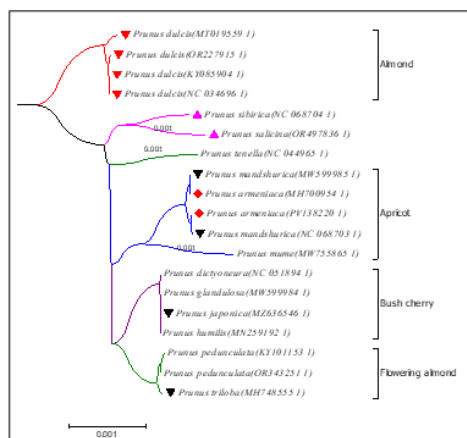


Figure 6a: Phylogram of Complete Chloroplast cp DNA Genomes of *Amygdalus (Prunus) dulcis* (157,723 bp DNA; NC_034696) and Related Species. Sequences were Downloaded from NCBI Server and the NJ Phylogram (Neighbor Joining) was Edited by NCBI/Distance of Results Application [37].

Main Clades, Significant Branch Length, Species Discussed in the Text, and the unit of Narrow Genetic Distance (0.001) are Labeled.

Chloroplast [41] DNAs (i.e., cp, pltd) Were also Investigated at the tRNA-Gly (trnG) Loci Which Allows Analysis of Almond Haplotypes of North American Native *Amygdalus / Prunus* Fasciculata (*Desert Almond*) (Figure 6b, c) and Related Species to the Eurasian Sweet Almond (*A. Dulcis*).

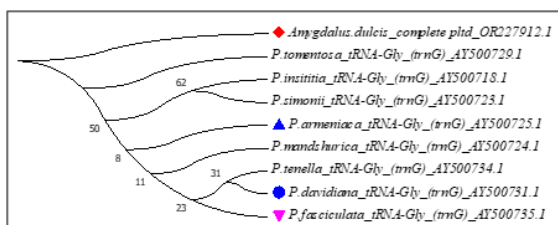


Figure 6b: Cp DNA Phylogram of a Single Gene at Trna-Gly (trnG) (>1,440 bpDNA) of Chloroplast Genomes of Sweet Almond (*Amygdalus dulcis*) (♦) and Related *Prunus* Species. APRICOT (*P. armeniaca*; ▲); *P. Davidiana* the Peach Ancestor (●); and *P. Fasciculata* (▼) (DESERT ALMOND, Evolved in North America; Figure 6/c.) are Labeled. ML Phylogram (Maximum Likelihood) was Edited by MEGA7 Computer Program [36]. Latin Names of Species, Gene Bank Accession Numbers, and Bootstrap Values (x1000 replicates) are Indicated.



Figure 6c: Native Almond Species of North America. (i) *Amygdalus Fasciculata* (DESERT ALMOND; <https://wildflowersofjoshuatreecountry.com>). (ii) *Prunus fremontii* (DESERT APRICOT) Harvested by Cahuilla Indians of the 52 Native American Tribes; <https://research.fs.usda.gov>). (iii) *P. Eremophila* (MOJAVE DESERT PLUM, described recently, 2001; <https://calscape.org>).

The tRNA-Gly phylogram (Figure 6b) showed independent lineages of *A. dulcis* and *A. fasciculata* which may indicate the 200 million year long parallel evolution in the chloroplast genomes of the two species growing in the two continents of Eurasia and Americas (Figure 6c).

Mitochondrial Genomes

The genomes of complete mitochondrial DNAs showed two main clades between *Prunus/Amygdalus* and *Malus* species (Figure 7).

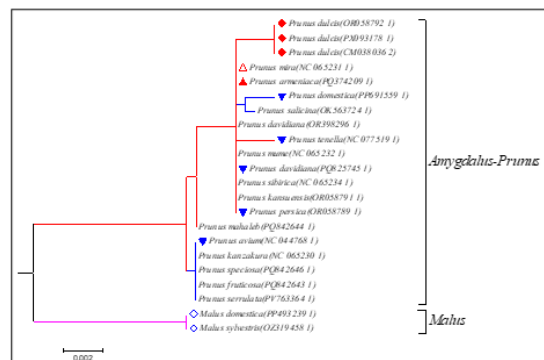


Figure 7: Phylogram of Complete Mitochondrial (MT DNA) Genomes Aligned to *Amygdalus (Prunus) dulcis* (444,092 BPDNA; M038036.2). Sequences Were Downloaded from NCBI Server [37] and the NJ Phylogram (Neighbor Joining) was Edited by the Application of NCBI/Distance of Results and Using a Sequence Rank of 1,000 bp MTDNAs. Species Discussed in the Text and the Unit of Genetic Distance (0.002) is Labeled.

Self (in)Compatibility (SI, SC) of Almond

Self-Pollination (i.e., inbreeding, selfing, self-fertilization) narrows plant genetic diversity (i.e., DNA sequence variability) which threatens plant tolerance against pathogens.

Several morphological (e.g., heterostyly) and molecular mechanisms evolved in wild plants to avoid self-pollination and allowed cross-pollination. One of these is self-incompatibility (SI) which bypasses plant self-compatibility (SC) [42,43]. However, plant breeders use inbred lines for yield improvement by hybrid vigor (i.e., heterosis) [44].

During self-incompatibility (SI), a plant's pistil recognizes and rejects its own pollen or pollen from a genetically similar plant. When pollens of the same plant reach pistils of the same flower the pollens cannot open pollen tubes towards ovary for they are digested by the plant own ribonuclease enzyme S-RNases (S stands for stigma of the carpel) which exudate on the surface of stigma of the style (e.g., stylar almond RNases; AY876939.1; 1,750 bpDNA, partial CDS). S-RNases show high level of DNA sequence diversity (i.e., 'allele diversity') [45] (Figure 8). Above this, pollens stuck on stigma express S-haplotype-specific F-box (SFB) proteins [46].

S-RNases show high level of sequence diversity (Figure 8) which indicates a recent evolutionary development. RNase genes in almond carries one or more long terminal repeat retrotransposons (LTRs) [47] which facilitate S-RNase gene mobility and copy number multiplication in the genomes [48,49].

The other type of SI caused by glycoprotein reaction was also identified in almond (e.g., AY743330.1; 602 bpDNA, partial cds).

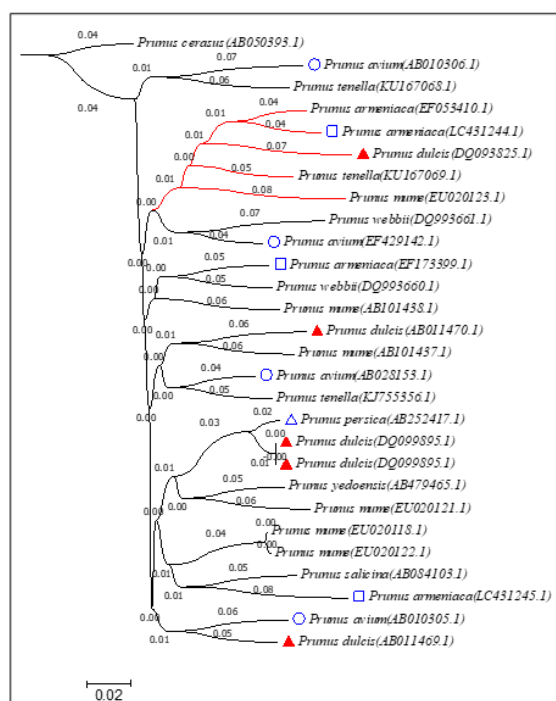


Figure 8: mRNA Phylogram (NJ, Neighbor Joining) of Nuclear S-RNase Genes with High Levels of Allele Diversities (i.e., Sequence Variations). *Amygdalus* (*Prunus*) *dulcis* Entries and Related Species Were Aligned to Almond (▲) mRNA (DQ099895.1; 826 Nt) and edited by NCBI/Distance Tree of Results. Latin Names, Gene Bank #s, Branch Length and Unit of Genetic Distance (0.02) are Indicated.



Figure 9: Sequences Alignments of Leucine-Rich Repeat Receptor-Like Protein Kinase (PEPR1a) Defense Genes (a Cell Surface Receptor Protein) of *Amygdalus dulcis* and Related Species (Samples of 48 NT Long DNA and 16 aa Protein of the >3,347 NTDNAS). Sequences were Aligned to Sequence of *Prunus persica* var. *nucipersica* (MW600846.1) by Clustal W Computer Program Inbuilt to Bio Edit (Accessory Application / ClustalW Multiple alignment), and Followed by File/Graphic View Application. Leucine (Leu) aa (in Red), the Synonymous- (in Blue) and Nonsynonymous Amino Acid Changes (in Green), Latin Names, and NCBI Entry Numbers are Indicated. Consensus DNA NTS are Dotted.

The most valuable almond cultivars are self-fertile - probably originating from cv. 'Touno' with inactive S-RNase genes and used by plant breeders. Dwarf almond (*A. nana*) always produce low nut set in climate of Central Europe and in Komi Republic (Asia) (which might correlate with SI function [10,50,51]).

Leucine-Rich Repeat Receptor-Like Protein Kinase (Pepr1a)
Similar to Arabidopsis, cell surface receptor proteins (PEP receptor1a, PEPR1a) the member of leucine-rich repeat receptor-like kinases LRR-RLKs (Figure 9) trigger defense signal transduction which also play important role in *Amygdalus* / *Prunus* species [52].

Functional Genomics

Apart from DNA sequence analysis, functional genomics allows gene expression (mRNA and protein) analyses. The transcription factor proteins (TFs) controll (activate or deactivate) gene expression leveles in natural way by binding to sequence-specific sites of the gene of study. Agronomically important traits, e.g., flowering time, fruit quality, cold hardiness, drought tolerance or disease resitances are controlled ny TFs. In peach (*Prunus persica*) great numbers of TFs (#1,533) were identified [8].

Several of them were found to be active in almond (*A. dulcis*) which regulate cold hardiness and drought tolerance. To compare, 1,600 TFs were identified in the human genome [53].

BHLH TFs. A point mutation (Leu to Phe) in the dimerization domain of bHLH2 (a basic Helix-Loop-Helix transcription factor/protein) gene was found to block transcription of the two first genes of the amygdalin (C20H27N1O11) biosynthesis (Figure 3) which resulted in sweet almond kernels during the evolution and allowed almond domestication. The mapped Sk gene of almond showed five BHLH1-5 genes [31].

CBF TFs. C-repeat-binding protein TFs of almond (BBH03298, 237 aa) controls cold hardiness the PdCBF1 (JQ317157; 2436 bpDNA) and PdCBF2 (JQ317158) [54].

MYB TFs. The polyphyletic oncogene viral avian MYeloBlastosis virus (AMV) TFs showed binding sequence site to MYB1 TFs [8].

In the pear genome (*Pyrus bretschneideri*) 129 PbMYB genes were identified, and two of them (PbMYB25 and PbMYB52) were found to control lignin biosynthesis during pear fruit development [55].

To compare MYB TFs sizes, the MYB25 is 202 aa in *Pyrus assuriensis* (XHH53721.1), and the MYB52 is 259 aa in *P. persica* (XP_020419093.1).

MYB domain protein-98 is 287 aa (BBH00425) in almond (Sánchez-Pérez et al., 2019).

Genome Edition

The Nobel Prized technology (Charpentier and Doudna, 2020: "for the development of a method for genomeediting ") was elaborated recently.

This breakthrough CRISP-Cas9 technology (Clustered Regularly Interspersed Palindromic repeats of DNAs) was based on a recently discovered new type of DNA restriction endonuclease Cas9 (CRISPR-associated proteins) which are guided by gRNA.

Discovery of Cas9 followed the former technologies of (i) zinc finger nucleases (ZFNs), (ii) transcription activator-like effector nucleases (TALENs), and the (iii) engineered array of sequence-specific DNA binding domains fused with DNA nuclease FokI [56].

The Cas9 DNA cutting enzyme was discovered by Feng Zhang in a bacterial defense mechanism against virus DNAs and plasmid DNAs (e.g., in *Streptococcus pyogenes*, SpCas9) [57,58].

To compare, Cas9c is 4,107 bpDNA, MK048158; 1,368 aa, QCQ82566. Later, an improved endonuclease cpfi/Cas12a was developed by [16]. Several observations preceded the technology developed by Feng, Z., Mojica, E.J.M.; Ishino, Y, Philippe Horváth; and Siksnys, V.

The CRISP-Cas9 technology is able to cut targetted DNA sequences, and the following DNA repair, DNA nucleotide changes occur which, after cloning to vector, followed by gene transfer to host plant or human genome, may result in new clones after a tedious work of selection. In the original paper of [56] more than 20 T₀ and 50 T₁ transgenic *Arabidopsis* plants were generated and selected [56].

This genome edition technology is already available to almond [61-67].

Methodology

Of the numerous synonym Latin names of sweet almond, the *Amygdalus dulcis* is used here and no systematic debates are discussed. Gene sequences were downloaded from servers of NCBI [63], and UNIPROT (2019) (www.uniprot.org) followed by sequence alignments by ClustalW computer program [38] inbuilt to NCBI server [37] and Bio Edit computer programs [39] according to [13] Phylogenetic NJ and ML phylograms were edited by computer program MEGA7 [36].

The Time Tree of Life phylogram were edited by TToL5 timetree.org server [62].

Conclusion

Almond (*Amygdalus dulcis*) was found here to have originated 51 MYA (million years ago). In North America wild almond species were developed by parallel evolution and analyzed here. Most of the nuclear-, cp-, and mtDNA sequence analyses clustered almond to individual clade, which indicate the use of the basic Latin name of *Amygdalus dulcis* instead of synonyms. The results presented in the current study may provide new data to geneticists and almond breeders to aid in the development of new varieties and hybrids with mold diseases resistances against *Monilia* and the aflatoxin producing *Aspergillus* coupled with increased yield. This genetic analysis may provide further data to breed new homozygous Sk/Sk sweet almond cultivars with tolerance to current (re)global warming and aridification coupled with early spring frosts of Northern temperate zone.

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