

The contribution of *Prunus webbii* to almond evolution

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Summary

The contribution of *Prunus webbii* to almond evolution

A Spanish population of *Prunus webbii*, first mentioned in 1977, shows great variation for morphological traits, pointing to the possibility of hybridization with cultivated almond. Most forms are self-compatible. Self-compatibility in *P. webbii* must be allelic with that of almond, as shown by the study of its transmission to hybrid seedlings, suggesting that self-compatibility in almond could be due to hybridization with *P. webbii*.

Key words: almond, hybridization, *Prunus webbii*, self-compatibility

Résumé

La contribution de *Prunus webbii* à l'évolution de l'amandier

Une population espagnole de *Prunus webbii*, mentionnée pour la première fois en 1977, montre une large variation de caractères morphologiques, ce qui présume la possibilité d'hybridation avec l'amandier cultivé. La plus part des formes sont auto-compatibles. L'auto-compatibilité chez *P. webbii* doit être allélique avec celle de l'amandier, comme montre l'étude de la transmission aux semis hybrides, ce qui suggère que l'auto-compatibilité chez l'amandier peut être due à l'hybridation avec *P. webbii*.

Resumen

La contribución de *Prunus webbii* a la evolución del almendro

Una población española de *Prunus webbii*, mencionada por primera vez en 1977, muestra una gran variabilidad en sus caracteres morfológicos, lo que apunta a una posible hibridación con el almendro cultivado. La mayoría de formas son autocompatibles. La autocompatibilidad en *P. webbii* debe ser alélica con la encontrada en el almendro, como se ve en su transmisión a los plantones híbridos, lo que sugiere que la autocompatibilidad en el almendro podría deberse a la hibridación con *P. webbii*.

Introduction

Some controversies have arisen about species identity and self-compatibility in the wild almond *Prunus webbii* (Spach) Vierh., as well as on its possible contribution to the origin of cultivated almond (*P. amygdalus* Batsch). Ladizinsky (1999) concluded that *P. webbii* was not a genuine wild type but a feral form derived from cultivated almond and that self-compatibility was not found in this taxon, suggesting that *P. webbii* had not contributed to the almond origin. Godini (2000) has already pointed out that *P. webbii* from the Italian region of Puglia is self-compatible and that probably contributed to the origin of the Puglia pool of almond cultivars. Similar conclusions can be reached from a Spanish population supporting a hypothesis contrary to Ladizinsky's conclusions. The objective of this article is to present the traits of the Spanish population of *P. webbii* in relation to the contribution of this species to almond evolution, mainly on the Mediterranean northern shore.

Almond origin

Although Ladizinsky's conclusion is that *P. fenzliana* is the most plausible ancestor of almond, the situation is complicated by the intermixing of the different wild almond species and the full crossability of most of them, as well as by the real consideration that some almond groves found in Central Asia, where many different wild species have been described (Browicz and Zohary 1996; Denisov 1988; Grasselly 1976), are feral or really wild (Popov et al. 1929). Socias i Company (1998a) suggests that origin of almond must take into account the contributions of many researchers who have looked attentively at the different almond species and their traits.

Almond was probably domesticated during the third millennium BC (Spiegel-Roy 1986). It has been suggested that domestication could have taken place in Central Asia

(Kovalyov and Kostina 1935) with *P. fenzliana* Fritsch., *P. bucharica* (Korsh.) Fedtsch., *P. kuramica* (Korsh.) Kitam. and *P. triloba* Lindl. probably involved in various hybridizations, giving rise to the current almond cultivars (Grasselly and Crossa-Raynaud 1980; Kester et al. 1990). Further, as almond cultivars moved towards the Mediterranean, new hybridizations might have occurred, especially with the wild Mediterranean species *P. webbii*, as already mentioned, resulting in some of the almond populations found along the northern shore of the Mediterranean sea from Greece and the Balkans to Spain and Portugal.

The genetic closeness of almond and peach led Watkins (1979) to suggest that both originated from the same primitive species but evolved separately following the mountain upheavals of the Central Asian massif. Thus, peach evolved in the east, spread over several regions of China, in a more humid climate and at lower elevations, whereas almond evolved in the west, in arid steppes, deserts and mountainous areas, under severe conditions that possibly led to its evolution towards self-incompatibility. Selection for domestication would have been for sweet kernel and larger nut size among these wild populations, which were propagated by seed.

Almond was presumably introduced into the Mediterranean area through seeds carried by caravans crossing the Central Asian steppes on their way from China to the West. This manner of dispersal has also been suggested for other fruit trees (Juniper et al. 1999) and would work in both directions. Gustafson et al. (1989) reported that the primary sources of almond at Kashgar, Xinjiang (China) were old seedling trees that had originated from Central Asia across the Tian Shan Mountains. Kashgar is on the old Silk Road connecting China and the West.

Based mainly on archaeological remains, Zohary and Hopf (1993) put forward another hypothesis for almond

origin, suggesting that it was taken into cultivation in the eastern part of the Mediterranean basin, more or less at the same time as the olive, grapevine and date palm. However, the wild populations and species found in this region are genetically more distant from the cultivated almond than the wild populations and species of Central Asia, throwing some doubts on this hypothesis. However, the introduction of almond into the eastern Mediterranean area was as early as the second millennium BC, because almond remains have been found in the tomb of Tutankhamon (Zohary and Hopf 1993). Almond cultivation must have existed in Greece long before the creation of the Greek myths to explain its incorporation into them (Graves 1955); also, there is evidence of almond trade in the western Mediterranean in the fourth century BC (Cerdá Juan 1973).

Traditional almond culture primarily utilized open-pollinated seedlings (Grasselly 1972; Rikhter 1972). This fact, together with self-incompatibility, has created a very high heterozygosity in this species, which is one of the most polymorphic fruit species (Kester et al. 1990; Socias i Company and Felipe 1992). This large variation has been an effective genetic pool for breeding, but at the same time has made more difficult the definition of its origin.

Distribution and morphological traits

According to Flora Europaea (1968), *P. webbii* grows in the southern part of the Balkan peninsula, the island of Crete and southern Italy, both on the mainland and on the island of Sicily (Grasselly 1976), but not in Spain. However, it was found in 1977 (Felipe and Socias i Company 1977) in the province of Toledo, at the centre of the region south of Madrid (Figure 1).

The Spanish population of *P. webbii* is found over several slopes of granitic origin, in apparently fully natural conditions, scattered with bushes and trees up to 4–5 m high. The most homogeneous population was found between the towns of Mora de Toledo and Tembleque (Figure 2), close to the river Algodor, a tributary of the Tajo river, one of the most important rivers of Spain. In addition, many other populations have been found in other locations, both on hills and shores of other rivers and non-permanent watercourses, and also at roadsides. In these cases, the shrubs were probably from natural dissemination of seeds by water, but in some cases also by man, as it has been found close to olive orchards where they have been seeded to grow as fences between fields due to their thorniness. These populations are much more heterogeneous, with a great variation of forms, from some closely resembling the cultivated almond, to others more like the wild type. Some local communicants have reported that some of these populations have disappeared owing to people from the nearby villages removing the wood for fire.

The fruits collected from several populations were all bitter and variable in size. The largest ones were even locally marketed and in some cases used to produce seedling rootstocks for almond, as also occurred with a Yugoslavian population (Vlasić 1977).

The range of variation found in these populations points to the possibility that most of them are not pure populations of *P. webbii*, but were produced by hybridization with the cultivated almond, which is grown in several places close to where the wild populations are found, but with no possibility of considering pure stands as scapes from *P. amygdalus*. Repeated hybridizations to one species or the other, as could have happened in Puglia, have produced this wide range of variation, while maintaining some typical traits of the wild type, such as the branching habit, leaf size and bitter kernels.

Self-compatibility

Special attention was paid to the study of self-compatibility owing to its importance in almond (Socias i Company 1990). Thus, several forms from different locations were studied according to their pollen tube growth (Socias i Company 1984). More than 90% of them were self-compatible, showing that this trait is variable, as well as some of the morphological traits as mentioned. Other studies on cross-compatibility were also carried out, showing that all the forms examined were



Figure 1. Location of the Toledo province in Spain.

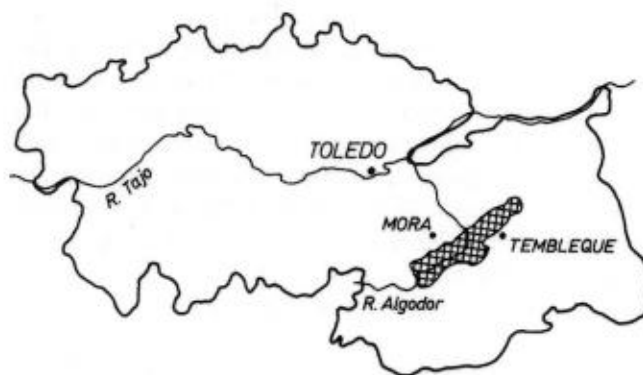


Figure 2. Location of the most homogeneous population of *P. webbii* in the province of Toledo.

cross compatible with each other, as well with cultivated almond. A special case is worth mentioning: a self-compatible form, as shown by the pollen tube growth, had all sterile flowers, with such a reduced ovary that the pistil hardly had any thickening at the base. Pollen, however, was fully viable, as shown both by its own tube growth and also that in other pistils.

Although Ladizinsky (1999) stated that self-compatibility was not found in *P. webbii*, Warfield (1968) had already studied a Yugoslavian population of *P. webbii*, showing again its self-compatibility and cross-compatibility with almond. *P. webbii* self-compatibility had also been suggested by Godini (1979) as a possible origin of self-compatibility in the almond population of Puglia. For this reason, a form from the Spanish population of *P. webbii* was crossed as a pollen parent with 'Tuono', the well-known self-compatible cultivar from Puglia. From this cross, 36 seedlings were studied for their self-compatibility. From those, 28 were self-compatible, four self-incompatible and four partially self-compatible. Following the criterion of Socias i Company (1984), the latter four were considered non self-compatible, giving a total amount of eight non self-compatible (Table 1).

'Tuono' is heterozygous for self-compatibility (Socias i Company and Felipe 1982) with a genotype S_1S_f (Crossa-Raynaud and Grasselly 1985), with S_f dominant over the S alleles of the self-incompatibility locus, according to the gametophytic self-incompatibility system in plants (Lewis and Crowe 1958). As the S locus is allelic in closely related species (Pandey 1968) and self-incompatible seedlings appear in this cross, this form of *P. webbii* must also be heterozygous for S_f . According to this hypothesis, the proportion of self-compatible to non self-compatible seedlings significantly agrees with the expected ratio of 3:1 (Table 1).

This implies that this form of *P. webbii* is probably of hybrid origin, being heterozygous for S_f , though *P. webbii* in origin must be self-compatible to give rise to this predominantly self-compatible population. This has possibly been the evolution of the almond population of Puglia as suggested by Godini (1979), where all the self-compatible almond cultivars identified (Godini 2002) have been shown to be heterozygous by NepHGE electrophoresis of pistil RNases (Bošković et al. 1999). Godini (2000) also points out some morphological similarities between *P. webbii* and some cultivars from Puglia as a support for this hypothesis.

Yamashita et al. (1987) found some specific protein bands peculiar to *P. webbii* from Puglia and 'Tuono' as compared with other almond cultivars by isoelectric focusing and SDS-PAGE, thus suggesting a close genetic relationship between

'Tuono' and the wild species, which could involve the transfer of self-compatibility from *P. webbii* to 'Tuono'. Unfortunately, this molecular approach has not been pursued. Although Martínez-Gómez et al. (2003) showed the genetic closeness of almond and *P. webbii*, they did not include 'Tuono' among the almond cultivars studied and the two *P. webbii* accessions are of unknown geographical origin. Channuntapipat et al. (2003) did include 'Tuono' in their identification of S alleles by PCR primers, and although S_f was identified in 'Tuono' as expected, it was not in the single *P. webbii* genotype included. However, this *P. webbii* form was from the Middle East, not from the Puglia region, where a possible identification of alleles would provide relevant information on the possible introgression of self-compatibility from *P. webbii* to cultivated almond.

There is an overlap of the distribution of *P. webbii* and the presence of self-compatible almond cultivars (Socias i Company 1990): the Puglia region (southern Italy), Bulgaria, Greece, Spain and Portugal. This overlap supports again the hypothesis of transmission of self-compatibility from *P. webbii* to almond.

There is another example of hybridization of almond involving self-compatibility; Socias i Company et al. (1976) found, in almond selections derived from almond×peach hybridization, different degrees of self-compatibility. They suggested that, even if the S_f allele from peach was allelic to the S series in almond, it could only be homoeologous and not completely homologous, with incomplete dominance in the hybrid offspring. Variations in the compatibility system could also occur because of the drastic change produced by shifting the S_f allele from a well coadapted system into a different coadapted system involving self-incompatibility. In addition, modifier genes influencing the major S locus could influence self-compatibility and be manifested to different degrees in these hybrids when two different genetic systems are put together. They also found female sterility owing to ovule abortion in some of the selections.

'Tuono' has a high proportion of flower sterility (Socias i Company 1983) and various degrees of female sterility have been observed among its progenies (Barahona and Socias i Company 1988). This parallels with the above selections studied by Socias i Company et al. (1976) and also relates to the presence of female sterile forms in the Spanish population of *P. webbii*. So, one can also consider the possibility of a natural transmission of self-compatibility from *P. webbii* to almond producing a genetic instability due to this hybridization, with female sterility and various degrees of self-compatibility.

Table 1. Number of self-compatible and non self-compatible seedlings obtained from the cross 'Tuono' × *P. webbii*

Phenotype	Observed	Expected	χ^2	p
Self-compatible	28	27		
Non self-compatible	8	9		
Sum	36	36	0.037	>0.95

Species identity

Although Ladizinsky (1999) concluded that *P. webbii* is a derived form and not a genuine wild type, the observations in several original sites and of the wild species collection of Zaragoza (Felipe 1984), point to it deserving a separate identity from the cultivated almond. However, as already mentioned, there is a wide cross-compatibility among the different almond species that can produce some confusion.

This cross-compatibility, on one side, reinforces the opinion that *Amygdalus* must be considered a subgenus in itself and not a full range genus, owing to the fact that Linnaeus had established restricted genera for the mostly European, well known species with common names, whereas the least known species were grouped in wider genera (Socias i Company 1998b). Thus, the stone fruits were classified in five different genera, a division that is probably too specified, and deserve to be classified as a single genus with different subgenera (Rehder 1940).

In contrast, the presence of intermediate forms, with a complete gradation from one species to the other, implies that the wild populations must be examined in full, in order to establish the traits of each species and recognise the intermediate forms as such and not as taxonomical subdivisions.

Conclusion

The Spanish population of *P. webbii* seems to be a hybrid pool, as shown by the morphological variability found and by the heterozygous condition for self-compatibility of some forms. However, the introgression of cultivated almond into this population must be small, as the general traits of the different populations fit quite well with the description of the wild species. Only for fruit size is there some deviation, as some forms have larger fruits than usual for *P. webbii*.

Self-compatibility in this species seems to be identical with that found in cultivated almond, as shown by the study of its transmission in hybrids of both species. This reinforces the hypothesis that self-compatibility in almond might have arisen by hybridization with *P. webbii*, thus stressing the contribution of *P. webbii* to the evolution of almond.

Acknowledgements

This research was supported by the Spanish projects RF02-001 of the Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA) and AGL2001-1054-C03-02 of the Comisión Interdepartamental de Ciencia y Tecnología (CICYT).

References

- Barahona M, Socias i Company R. 1988. Esterilidad floral en distintas descendencias de almendro. III Congreso Nacional Sociedad Española Ciencias Hortícolas, Tenerife, p. 119.
- Bošković R, Tobutt KR, Duval H, Batlle I, Dicenta F, Vargas FJ. 1999. A stilar ribonuclease assay to detect self-compatible seedlings in almond progenies. *Theoretical and Applied Genetics* 99:800–810.
- Browicz K, Zohary D. 1996. The genus *Amygdalus* L. (*Rosaceae*): species relationships, distribution and evolution under domestication. *Genetic Resources and Crop Evolution* 43:229–247.
- Cerdá Juan D. 1973. Economía antigua de Mallorca. In: Mascaró Pasarius J, editor. *Historia de Mallorca*, vol. I. J. Mascaró Pasarius, Palma de Mallorca, pp. 417–448.
- Channuntapipat C, Wirthensohn M, Ramesh SA, Batlle I, Arús P, Sedgley M, Collins G. 2003. Identification of incompatibility genotypes in almond (*Prunus dulcis* Mill.) using specific primers based on the introns of the S-alleles. *Plant Breeding* 122:164–168.
- Crossa-Raynaud P, Grasselly C. 1985. Éxistence de groupes d'interstérilité chez l'amandier. *Options Méditerranéennes CIHEAM/IAMZ 85/I:43–45*.
- Denisov VP. 1988. Almond genetic resources in the USSR and their uses in production and breeding. *Acta Horticulturae* 224:229–236.
- Felipe AJ. 1984. État de l'arboretum des espèces sauvages d'amandier à Saragosse. *Options Méditerranéennes CIHEAM/IAMZ 84/II:203–204*.
- Felipe AJ, Socias i Company R. 1977. Un amandier sauvage, probablement *A. webbii*, non encore mentionné en Espagne. III Colloque GREMPA, Bari, 3–7 Octobre 1977, pp. 78–79.
- Flora Europaea. 1968. *Flora Europaea*. Volume 2. Cambridge University Press, Cambridge, UK.
- Godini A. 1979. Ipotesi sulla comparsa dell'autocompatibilità nel mandorlo. *Rivista di Scienza e Tecnica Agraria* 19(2/3):3–10.
- Godini A. 2000. About the possible relationship between *Amygdalus webbii* Spach and *Amygdalus communis* L. *Nucis* 9:17–19.
- Godini A. 2002. Almond fruitfulness and role of self-fertility. *Acta Horticulturae* 591:191–203.
- Grasselly C. 1972. L'amandier: caractères morphologiques et physiologiques des variétés, modalité de leurs transmissions chez les hybrides de première generation [thesis]. University of Bordeaux.
- Grasselly C. 1976. Les espèces sauvages d'amandier. *Options Méditerranéennes*. 32:28–43.
- Grasselly C, Crossa-Raynaud P. 1980. L'amandier. G.P. Maisonneuve et Larose, Paris, XII+446pp.
- Graves R. 1955. *The Greek myths*. George Braziller, New York.
- Gustafson WA, Morrissey TM, Bish C. 1989. Plant exploration and germplasm collection of cold hardy woody plants for Nebraska from the People's Republic of China. University of Nebraska, Lincoln, Neb.
- Juniper BE, Watkins R, Harris SA. 1999. The origin of the apple. *Acta Horticulturae* 484:27–33.
- Kester DE, Gradziel TM, Grasselly C. 1990. Almonds (*Prunus*). *Acta Horticulturae* 290:699–758.
- Kovalyov NV, Kostina KF. 1935. A contribution to the study of the genus *Prunus* Focke. Questions of taxonomy and plant breeding [in Russian]. *Trudy po Prikladnoj Botanike Genetike Seleksie Series* 8(4):1–76.
- Ladizinsky G. 1999. On the origin of almond. *Genetic Resources and Crop Evolution* 46:143–147.
- Lewis D, Crowe LK. 1958. Unilateral interspecific incompatibility in flowering plants. *Heredity* 12:233–256.
- Martínez-Gómez P, Arulsekhar S, Potter D, Gradziel TM. 2003. Relationships among peach, almond, and related species as detected by simple sequence repeat markers. *Journal of the American Society for Horticultural Science* 128:667–671.
- Pandey KK. 1968. Compatibility relationships in flowering plants: role of the S-gene complex. *American Naturalist* 102(927):475–489.
- Popov MG., Kostina KF, Poyarkova AI. 1929. Wild trees and shrubs in Central Asia [in Russian]. *Trudy po Prikladnoj Botanike Genetike Seleksie* 2:241–483.
- Rehder A. 1940. *Manual of cultivated trees and shrubs*. Macmillan, New York, 996pp.
- Rikhter AA. 1972. Biological basis for the creation of almond cultivars and commercial orchards [in Russian]. *Glavny Botanicheskij Sad, Moscow*.
- Socias i Company R. 1983. Flower sterility in almond. *Acta Horticulturae* 239:69–74.
- Socias i Company R. 1984. A genetic approach to the transmission of self-compatibility in almond (*Prunus amygdalus* Batsch). *Options Méditerranéennes CIHEAM/IAMZ 84/II:123–127*.
- Socias i Company R. 1990. Breeding self-compatible almonds. *Plant Breeding Reviews* 8:313–338.
- Socias i Company R. 1998a. Fruit tree genetics at a turning point: the almond example. *Theoretical and Applied Genetics* 96:588–601.
- Socias i Company R. 1998b. La taxonomie de l'amandier. *Cahiers Options Méditerranéennes* 33:91–93.
- Socias i Company R, Felipe AJ. 1982. Transmission of self-compatibility in almond. Abstracts XXI International Horticultural Congress 1:1150.

- Socias i Company R, Felipe AJ. 1992. Almond: a diverse germplasm. *HortScience* 27:717-718, 863.
- Socias i Company R., Kester DE, Bradley MV. 1976. Effects of temperature and genotype on pollen tube growth of some self-incompatible and self-compatible almond cultivars. *Journal of the American Society for Horticultural Science* 101:490-493.
- Spiegel-Roy P. 1986. Domestication of fruit trees. In: Barigozzi C, editor. *The Origin and Domestication of Cultivated Plants*. Elsevier, Amsterdam, pp. 201-211.
- Vlasić A. 1977. *L'Amygdalus webbii* (Spach) ed i suoi ibridi con pecco come portainnesto del mandorlo. III Colloque GREMPA, Bari, 3-7 Octobre 1977, pp. 80-81.
- Warfield DL. 1968. An investigation of a Yugoslavian *Prunus* introduction of potential value in almond breeding [MS Thesis]. University of California, Davis.
- Watkins R. 1979. Cherry, plum, peach, apricot and almond. *Prunus* spp. In: Simmonds NW, editor. *Evolution of Crop Plants*. Longman, London, pp. 242-247.
- Yamashita K., Gaude T, Dumas C, Grasselly C, Crossa-Raynaud P. 1987. Protein analysis on pistils and pollens of almonds with special reference to Sf, a self-fertile gene. *Journal of the Japanese Society for Horticultural Science* 56:300-305.
- Zohary D, Hopf M. 1993. *Domestication of plants in the old world*. Clarendon Press, Oxford.

Plant Genetic Resources Newsletter

Bulletin de Ressources Phytogénétiques

Noticiario de Recursos Fitogenéticos



No. 140, 2004



**Food and Agriculture Organization of the United Nations and the
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l'institut international des ressources phytogénétiques
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