On the origin of almond

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Abstract

Almond, Amygdalus communis L., is an ancient crop of south west Asia. Selection of the sweet type marks the beginning of almond domestication. Wild almonds are bitter and eating even a relatively small number of nuts can be fatal. How man selected the sweet type remains a riddle. Also, the wild ancestor of almond has not been properly identified among the many wild almond species. Breeding experiment, which is the most critical test for identifying the wild progenitors of other crops, is ineffective in almond, because it is interfertile with many wild taxa. The so-called wild A. communis of central Asia cannot be regarded as a genuine wild form, but as a feral form, or remains of old afforestation. The wild taxa morphologically akin to almond, A. korshinskyi (H.-M.) Bommi. and A. webbi Spach, are also feral types occurring in the Middle East and southern Europe, respectively. The taxon A. fenzliana (Fritsch) Lipsky is the most likely wild ancestor of almond for three reasons: 1. It is a genuine wild type forming extensive thickets of large trees young seedlings and all the intergradations between them in nature; 2. Its morphology, and particularly the partially pitted grooved nut-shell are within the range of variation of almond, and 3. A. fenzliana is native of Armenia and western Azerbaijan in the Middle East where almond was apparently domesticated.

Introduction

Almond is one of the oldest nut crops of south west Asia, and from that region it has diffused to other regions and continents. The most ancient, 19,000 bp, remains of almond are two 2 mm nut-shell fragments recovered in Ohalo, on the shore of the Sea of Galilee, Israel (Kislev et al., 1992). If these are indeed almond remains, they must be of a wild form because agriculture in that area began about 10,000 years later. Bronze Age 3200 BP, almond nut-shell remains from Nuremria, Jordan (McCreery, 1979) are believed to be of domesticated almond because they were found together with domesticated wheat and barley and parched grapes. Despite the antiquity of the almond crop, its wide distribution and economic importance, we still lack basic information on the process of its domestication, its wild progenitor and the area in which domestication had happened. The present article intends to elucidate some of the problems of almond domestication and to suggest the taxon which is the most likely the almond wild progenitor.

The riddle of almond domestication

Cultivated almond nuts are sweet, though occasionally individual trees in traditional almond orchards bears bitter nuts which are not edible. All the wild almond taxa bear bitter nuts, sweet type may occur, but in a very low frequency. The bitter taste is due to the presence of the glucoside amygdalin which following mechanical damage to the kernel is transformed into the deadly prussic acid (hydrogen cyanide). Besides the bitter taste, the consumption of a small quantity of bitter almonds, several dozens in one sitting, may be fatal. Hence, bitter almond could not be a source of food for human before the selection of the sweet type. The sweet type is controlled by a single dominant gene and domesticated almond cultivars may be homozygous or heterozygous to this gene (Heppner, 1923, 1926). I have tried to remove the bitterness
by leaching, boiling and roasting but without success, which further suggests that it is inconceivable that wild almond had been used as a source of food for humans before sweet type was selected. The intriguing question is how the sweet type was detected after all. A sweet type in a genuine wild almond population may arise from a mutation in the sweet gene. The mutation rate in that particular gene is not known, but if it is in the range of $10^{-5}$-10^{-6}, as is the rate in many other genes, sweet varieties must be extremely rare. The rarity of sweet types in genuine wild almond stands also suggests that they are selectively inferior to the bitter type. Since sweet types can be identified only by testing, one has to chew nuts from hundreds of thousands of bitter almond trees before finding the sweet type. Also, eating immature fruits (drupes), which is common in places where almond is a crop, could not account for the detection of sweet types in wild almond, because the bitterness is present already in young fruits. While it is difficult to see how a sweet type could be detected in wild stands, it is equally puzzling why man would plant useless bitter almond trees in his backyard and then select a sweet type among them. Planting wild almond trees as ornamental is a possible reason, because almond is one of the first woody species flowering in the spring, albeit for a short period.

Even when a sweet type had been found, its reproduction presented a problem. Unlike other Old World fruit trees, fig, grapevine, pomegranate, olive and date palm, which can be reproduced vegetatively: the first three by cuttings, olive by suckers and date palm by suckers, and specific clones can be maintained, almond is reproduced only by seeds. Almond is a gametophytically self incompatible organism, and when a heterozygous sweet type mutant is pollinated by a bitter type it produces seedlings of sweet and bitter types at a 1:1 ratio. This problem is still common in places where almond is reproduced from seeds and occasionally individuals bearing bitter nuts are recovered from nuts collected on heterozygous sweet types.

The difficulty of identifying the almond's wild ancestor

Traditionally, the identification of a crop's wild progenitor is based on morphological similarity and more so upon their interfertility with the crop, namely, the ability to produce viable and fertile F1 hybrids with the crop with no hybrid breakdown in the segregating generations. The breeding experiment is essential, because genetically a crop and its wild progenitor are members of the same species. Although it is fashionable nowadays to suggest ancestry by similarity in molecular markers between the crop and the related wild species, these comparisons alone are not equate for positive and ultimate identification of wild progenitors.

Breeding experiments:

For almond, breeding experiments are ineffective for the detection of its wild progenitor. This because almond is cross fertile with almost all wild almond taxa and natural hybrids are common wherever almond is grown adjacent to wild almonds. Some of these hybrids have even been described as new species (see Browicz and Zohary, 1996). I have personally observed such spontaneous fertile hybrids involving almond and the wild species A. bucharica Korsh. and A. spinosissima Bge., in Uzbekistan, A. orientalis Dula., and A. graeca Lindl. in Turkey. Denimen (1990) mentioned fertile spontaneous and artificial hybrids between almond and A. arabica Oliv. and A. fenzliana, and rare spontaneous hybrids with A. pekinense L. The potential gene flow between almond and wild species of the genus Amygdalus suggests that some of the reports of sweet types in wild almond species are products of introgression and not genuine mutations. Free gene flow is not restricted to cultivated and wild almond taxa and can be detected in places where two wild forms grow side by side. In Uzbekistan for example, A. spinosissima grows in elevations of 600-1500 m, and A. bucharica usually grows in higher elevations (900-2700 m), and hybrids between them occur when they grow side by side. At an altitude of about 1500 m, on the road between Samarkand and Shakhrizabad, southern Uzbekistan, A. spinosissima, a thorny shrub with small leaves and drupes, and A. bucharica, a tree with relatively large leaves and drupes with typical stone shape, form a mixed stand and hybrids can be recognized by various combinations of leaf shape, thorniness and drupe shape and size. Using these criteria, I have identified about 2% of the individuals as hybrids or hybrid derivatives. The free gene flow between the various taxa of Amygdalus makes them all members of one polymorphic biological species. It is, however, convenient to keep some of them as separate entities, perhaps as subspecies, because many of them show distinct morphology, distribution and ecology.

The free gene flow is not unique to members of the genus Amygdalus, but also include a member of the genus Prunus, i.e. P. persica, the peach. Almond and