Wild apples and wild pears

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Abstract

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The principal wild progenitors of the cultivated apples and pears grown in Europe and west Asia are the crab apple (*Malus sylvestris* (L.) Miller, and wild *Pyrus communis* L. subsp. *communis* = *P. pyraster* Burgst.). Both are widely distributed over Europe and southwest Asia. The wild primary gene pools of these fruit crops are, however, much wider. They include most (and perhaps all) of the congeneric wild relatives of these crops.

Introduction

For the following reasons the wild relatives of apple and pear are attractive candidates for assessing the needs for conservation of wild genetic resources of fruit crops in Europe:

(1) Economically, cultivated apple and pear rank among the most important fruit crops grown in Europe. They also carry considerable economic weight in the temperate parts of the other continents of the World.

(2) Apple and pear are native crops of Europe. Their closest wild relatives are widely distributed over this continent. Also the patterns of morphological variation, the geographic distribution, and the reproductive biology of these wild relatives are well known. So are the crossing relationships between them and their cultivated counterparts.

(3) Both apple and pear represent cases — not uncommon among fruit crops — in which the crop crosses freely not only with its closest wild relatives, but also with most of its more remote, con-generic relatives. Indeed, in apple and in pear, dozens of widely diverged wild species are inter-fertile with the fruit crops; and a whole genus (containing dozens of species) constitutes the primary gene-pool of the cultivated fruit tree. Such enormous, easy-to-tap, wild gene-pool is a real blessing for the apple and pear breeders.

Conservationists, on their part, have to make up their minds what to protect and how to conserve such vast wild genetic resources.

Apple: *Malus domestica*

The cultivated apple *Malus domestica* Borkh. (= *M. pumila* Miller), is a native European and west Asiatic fruit tree. The fruit crop thrives in areas where the winters are sufficiently cool to provide the trees with a chilling phase necessary for breaking bud dormancy. As in most fruit crops, apple cultivation is based on a shift from sexual reproduction (in the wild) to vegetative propagation by grafting (under domestication). Several thousands cultivars are recognized in this fruit crop. Many are diploid ($2n = 2x = 34$) and self-incompatible, i.e. resemble, in these features, their wild progenitors. Under domestication, triploid ($2n = 3x = 51$) and tetraploid ($2n = 4x = 68$) self-compatible apple clones have evolved as well.

The genus *Malus* (excluding *Eriolobus*) comprizes about 30 species (Rehder 1940, Watkins 1986, Way & al. 1991) as well as numerous interspecific hybrids (many of which were given binomials). The wild members of this genus are distributed over the temperate regions of Europe (a single wild species), Asia (the majority of the species), and North America (several species). East Asia is particularly rich in species (Rehder 1940, Watkins 1986). Most of the wild species are diploid ($2n = 2x = 34$), sexually reproducing and self-incompatible (Watkins 1995). Few wild taxa are apomictic and either triploid or tetraploid; very few wild forms are sexually reproducing and tetraploid (Way & al. 1991, Watkins 1995). Numerous crosses have already been made between various *Malus* species, and almost all of them resulted in fully fertile inter-specific hybrids. The diploid varieties of the cultivated apple seem to be cross-fertile with most (perhaps all) the sexually reproducing wild *Malus* species. (For a list of such successful inter-specific crosses see Way & al. 1991).

The wild 'crab apples' of the temperate parts of Europe, northern Anatolia and the Caucasus show the closest affinities to the crop (Zohary & Hopf 1993: 163). These widely distributed wild apples (Fig. 1) are usually referred to in the taxonomic literature as *M. sylvestris* (L.) Miller. Similar to many other widely distributed temperate trees, *M. sylvestris* shows considerable ecological and geographic differentiation. A distinct west-to-east cline occurs in these wild crab apples, which justifies their subdivision into two principal geographic races: (i) a western race, subsp. *sylvestris*, native to Europe, and (ii) an eastern race subsp. *orientalis* (Uglitzkich.) Browicz (= *M. orientalis* Uglitzkich), native to north Turkey and the Caucasus. The western subsp. *sylvestris* is widely spread in west, central and east Europe, occupying a wide range of altitudes — from sea level plains to almost sub-alpine sites. It penetrates north as far as south Scandinavia. All over this vast geographic range (Fig. 1), these wild apples thrive as components of deciduous and coniferous forest formations (including lowland woods), and grow on a wide variety of soils. In addition, the wild crab apples (occasionally also hybrid derivatives between wild forms and the domestic apples and/or feral apples) colonize man-made habitats. Quite frequently they grow at the edges of cultivation, or find refuge in hedges. They are diploid ($2n = 2x = 34$) and self-incompatible. As many other Rosaceous trees, wild *M. sylvestris* is pollinated mainly by bees; and reproduces entirely by seeds.

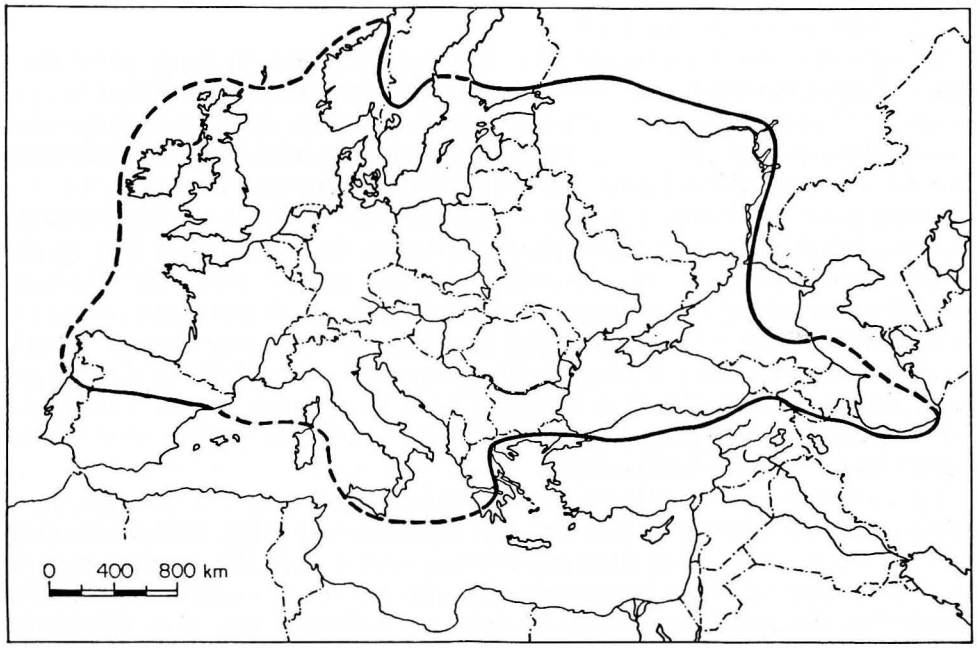

Fig 1. The distribution area of the wild crab apple *Malus sylvestris* (L.) Miller.

Under traditional farming practices, wild crab apples have been also commonly used as rootstock for grafting domestic clones.

As argued by Zohary and Hopf (1993: 166), the available evidence — from the living plants, from archaeology and from early written sources — implicates *M. sylvestris* as the principal wild progenitor from which the European, Near Eastern and Caucasian apple cultivars could have evolved.

Yet, one has to keep in mind that *M. sylvestris* is not the sole wild contributor to the crops gene-pool. Several additional *Malus* species (Watkins 1986) seem to have enriched the variation in this fruit crop through secondary hybridization. In central Asia, for example, the contribution of the native wild species *M. sieversii* (Ledeb.) M. Roem., seem to be considerable; and the local apple cultivars frequently manifest *M. sieversii* traits. (They are also frequently grafted on *sieversii* rootstock).

If indeed apple domestication took place in Europe and/or west Asia, and only later diffused to central Asia, introgression from the hardy *M. sieversii* could have greatly helped the introduction of this fruit crop to the harsh enviroment of central Asia. Similarly, further east, *M. prunifolia* (Willd.) Borkh. and *M. baccata* (L.) Borkh. (both cold resistant species native of north China and east Siberia) seem to have contributed significantly to the crop's local gene-pool. More recently, by the use of controlled breeding, several other *Malus* species have been crossed with the crop, especially to introduce resistance to diseases, pests and climatic stresses, and to develop superior rootstocks (Watkins 1986, Way & al. 1991).

Pear: *Pyrus communis*

The cultivated pear of Europe and West Asia, *Pyrus communis* L. subsp. *sativa* (DC.) Hegi (= *P. domestica* Med.) is second to the apple in its contribution to fruit production in the temperate parts of Europe. Similar to the apples, also pears show very wide variation under domestication, and more than a thousand cultivars have been recognized in this fruit crop. Pears too need winter chilling to ensure normal flowering and fruit setting.

The picture of domestication in *Pyrus* is complicated by the fact that in addition to the European pear *P. communis* L. (domesticated in Europe and/or west Asia), other species of pear were independently taken into cultivation in East Asia (Watkins 1986). The latter gave rise to the cultivated Chinese sandpear, *Pyrus pyrifolia* (Burm.) Nakai, and to the Chinese white pear, *P. bretschneideri* Rehd. Until last century, this had nothing to do with European horticulture. But since then the Far East pears were introduced into Europe and North America, and crossed with *P. communis*. Some modern pear cultivars already have had a polyphyletic origin. They are products of hybridization between the western and the eastern cultivated stocks (Watkins 1986).

According to Browicz (1993), the genus *Pyrus* L. contains some 38 known species, as well as numerous interspecific hybrids (many of which were given binomial botanical names). The wild members of *Pyrus* are distributed over Europe, the temperate parts of Asia, and north-west Africa. Browicz also notes that because of extensive inter-specific hybridization (particularly in the Caucasus and in the Balkans) a clear-cut delimitation of species in this genus is a difficult task. Very likely the actual number of good species in *Pyrus* is much smaller than the number given in his list. The infra-generic structure of *Pyrus* is, however, clear: Most workers subdevide the genus into the following two sections:

(1) Sect. *Pyrus* (which includes *P. communis*), in which the fruits have persisting sepals and are borne on relatively thick and short pedicels. This is, geographically, the western group of pears. Its members are distributed over west, central and south Europe, northwest Africa and southwest Asia from Anatolia to the Caucasus to Turkmenia — with extension to Tyan Shan mountain range and north Afghanistan. Richest in species belonging to this section are the Caucasus and Anatolia.

(2) Sect. *Pashia* Koehne, in which the fruits coat has numerous whitish lenticels, the pedicels are long and thin, and the sepals do not persist on the fruit. This is essentially an east Asiatic group. Its members are distributed over the Himalayas, north Vietnam, central and eastern China, Korea, Japan, and extend north to the Russian Far East. A single member occurs in the Hyrcanian forest zone, opposite the south coast of the Caspian Sea. Section *Pashia* includes *Pyrus pyrifolia* (Burn.) Nakai and *P. bretschneideri* Rehd., the sand pear and white pear of the Far East.

All *Pyrus* species seem to be self-incompatible (Zielinski 1965); all have the same diploid ($2n = 2x = 34$) chromosome number. The only exceptions are some tetraploid ($2n = 4x = 68$) cultivated clones (Watkins 1995). Numerous inter-specific crosses have been performed also in this genus. All produced fertile hybrids.

These results indicate that similar to the apples, *Pyrus* species are not reproductively isolated from one another by cross-incompatibility, hybrid inviability or hybrid sterility; but only by geographic and ecological isolation barriers. This explains why, when different *Pyrus* species come in contact, they tend to massively hybridize. On the other hand, the lack of hybrid inviability or hybrid sterility in inter-specific crosses in *Pyrus* is a great bonus for the pear growers. As in *Malus*, the whole genus constitutes an enormous, easy-to-tap primary gene-pool; both for the breeding of novel cultivars, and for the development of better rootstocks.

The cultivated European pear *Pyrus communis* L. (= *P. domestica* Med.) has its closest taxonomic affinities with a variable aggregate of wild pears distributed over the temperate parts of Europe, Turkey, the Caucasus, as well as north-west Africa (Fig. 2). Some workers (see for example Browicz 1993 conspect) place both the cultivated European pear and these wild pears in a single collective species, *P. communis* L., and regard the main wild variants as wild subspecies. Others maintain the wild forms separate, commonly referring to them as *P. pyraster* Burgst. Several other pear taxonomists even split the wild aggregate into several species. The available evidence — from the living plants, archaeological digs and from early written sources — strongly implicates these European, Anatolian and Caucasian wild pears as the principal wild stock from which the European fruit crop could have evolved (Zohary & Hopf 1993: 166).

This evidence further justifies the inclusion of all these intergrading cultivated and wild pears in a single collective species.

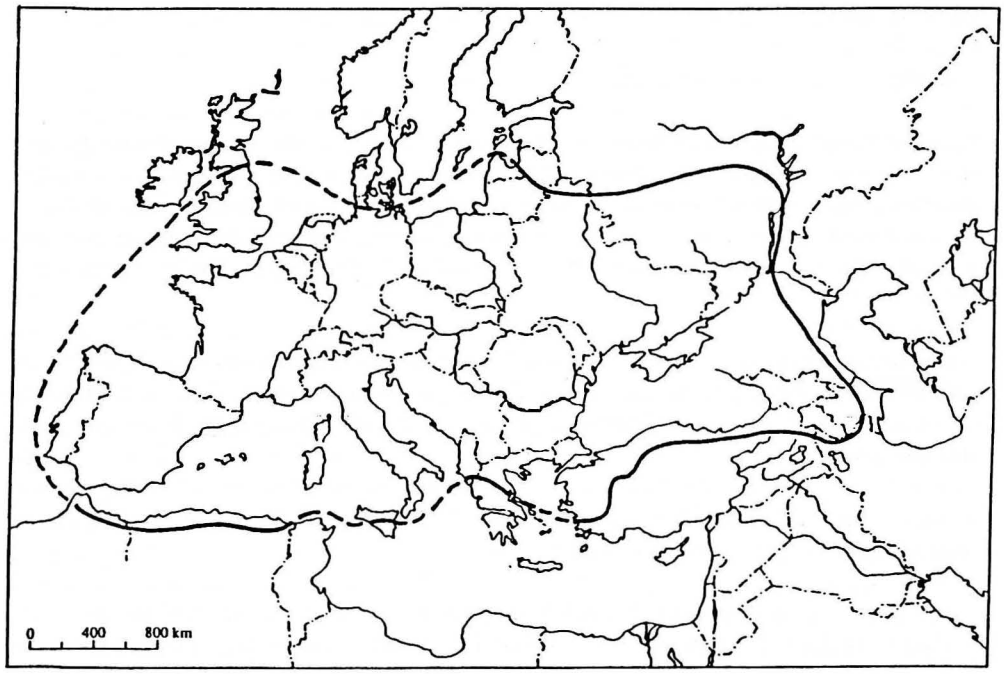

Fig. 2. The distribution area of wild forms of the Europan wild pear *Pyrus communis* L.

Browicz (1993) grouped the wild forms of *P. communis* in the following wild subspecies:

(1) *P. communis* L. subsp. *communis* (= *P. pyraster* Burgst.; *P. achras* Gaertner), which is widespread over the temperate parts of Europe. (Browicz maintains that this is the right botanical name for the European *pyraster*-type wild pears, while the cultivated varieties should be called *P. communis* L. subsp. *sativa* (DC.) Hegi).

(2) *P. communis* L. subsp. *caucasica* (Fed.) Browicz (= *P. caucasica* Fed.), which replaces the first wild subspecies in Thrace, Krym, north Anatolia and particularly in the Caucasus.

(3) *P. communis* L. subsp. *rossica* (Danilov) Tuz., which occurs in Kursk and Voronezh districts of Russia.

(4) *P. communis* L. subsp. *mamorensis* (Trabut) Maire (= *P. marmorensis* Trabut), native to the Atlantic coastal belt of Marocco.

(5) *P. communis* L. subsp. *longipes* (Cosson et Durand) Maire (= *P. longipes* Cosson et Durand), native to Algeria.

(6) *P. communis* L. subsp. *gharbiana* (Trabut) Maire (= *P. gharbiana* Trabut), native to Algeria.

Also several other European wild pear variants, i.e. the *P. cordata* Desv., growing in the western margins of Europe; and *P. nivalis* Jacq., from south and south-central Europe do not seem to represent independent pear species — but only wild races of *P. communis*. Both these variants fully intergrade with the *pyraster*-type pears.

In Europe (Browicz 1992), the wild forms of *P. communis* are particularly common in the central and eastern parts of the continent. They get rarer towards the warmer south where they are confined to relatively mesic and elevated spots. The *pyraster*-type wild pears are mesophyllous trees that can attain up to 28 m. in height. They occur both in deciduous and coniferous forests, mostly in lowlands (up to an elevation of 1000-1100 m.), and they favour forest edges and similar less shaded places. In addition, they also colonize places opened up by man, edges of cultivation (including hedges), and roadsides.

All in all, the morphological diversity and ecological range of the wild *P. communis* aggregate in Europe is considerable. In the south this variation is further enriched by the appearance of the following additional wild *Pyrus* species, which grow in more xeric Mediterranean or steppe environments; and — as already mentioned — are also cross-fertile with the crop.

(1) *P. spinosa* Forssk. (= *P. amygdaliformis* Vill.). This wild pear is widespread in the Aegean belt (including Crete) and in the south Balkan (Browicz 1982), thriving in park-forests, degraded forests and maquis-type Mediterranean vegetation and at edges of cultivation. This wild pear also extends to south Italy, and probably to south Spain.

(2) *P. eleagnifolia* Pallas. This is primarily an Anatolian steppic element (Browicz 1982), which extends to Thrace, east Bulgaria and Krym. It dots the landscape of steppe and steppe-like environments in these countries, including edges of cultivation.

Genetic connections between the crops and their wild relatives

In numerous places in Europe and Asia apple and pear cultivation is being practiced in areas supporting wild populations of *Malus* and *Pyrus* species. Quite frequently such wild stands grow in close proximity to plantations of these fruit crops. Because both in *Malus* and in *Pyrus* the crops and their wild relatives are self-incompatible and fully inter-fertile, spontaneous hybridization between tame and wild is rather common. Wild-looking apple or pear populations, growing in contact places, commonly include rare intermediate individuals and show morphological signs of introgressive hybridization. This is particularly true when such stands colonize disturbed habitats such as road sides or edges of cultivation. Sometimes fully developed hybrid swarms are encountered. Such spontaneous hybridization idicates that the diffusion of the crops (by man) over Europe and Asia, brought the cultivated apple and pear in contact with new wild relatives. In other words, the spread of horticulture superimposed the cultivated fruit trees over many of their previously geographically separated wild relatives, and resulted in new genetic connections. Exactly how extensive has been this gene-flow between the cultivars and their cross-fertile wild relatives is still hard to assess. Yet the available (mostly morphological) clues seem to indicate that it has been considerable. As already noted, in new territories, introgression from native wild relatives seems to have facilitated the the build up of locally adapted cultivars. On the other hand it very probably also helped the development of weedy apple and pear populations, which sometimes colonize edges of cultivation and other human-made habitats.

The impact of modernization

Under traditional farming practices, individuals of wild forms of *P. communis* as well as those of *Malus communis*, *P. eleagnifolia* and *P. spinosa* were commonly spared by the farmers when they cleared forests or collected firewood. As was the case with several other wild fruit trees, wild apples and pears were frequently left to grow in cleared places and at the edges of cultivation. Also their main branches were sometimes grafted with domestic clones. Occasionally farmers left such wild fruit tree individuals even inside their cultivated fields. Thus until recently such tolerated wild pears and apples dotted the agricultural landscape in many places in Europe and southwest Asia (particularly in the Balkan, Anatolia and the Caucasus). As Zagoja (1983) stressed, with the introduction of mechanized farming and modern transportation this practice is now quickly disappearing. In most places such wild fruit trees have already disappeared.

Conclusions

This review aims to show how variable and how complex the primary wild gene-pools of the apple and pear are. It also stresses the fact that the principal wild progenitors of these two important fruit crops are distributed over much of Europe. Although the survival of the wild apples and pears in Europe seems not yet critically threatened, their wild habitats on this continent are shrinking as a result of urbanization and industrialization. Also the relative tolerance towards these wild fruit trees which was part of the old type land use is rapidly disappearing.

The general geographic distribution, and the main patterns of the morphological differentiation in the wild pears and apples in Europe are already relatively well known. What we still badly lack are the following elements of information:

(i). More detailed chorological and demographic accounts on the wild apples and pears, their ecology and their habitat preferences in the various European countries; and an estimate on the damage already inflicted (or to be soon inflicted) on their habitats.

(ii). Basic information (either by the use of isozymes or DNA markers) on the range of genetic variation in the wild relatives of the apple and the pear over their distributional areas, and the structuring of this variation both between and within populations.

Only after obtaining such information one could more critically assess the threats to the wild apples and pears in Europe, and identify the species, subspecies and/or other wild variants that need (or will soon need) protection.

References

Browicz, K. 1982: Chorology of trees and shrubs in south-west Asia and adjacent regions. **1**. — Institute of Dendrology, Polish Academy of Sciences, Kornik, Poland.

— 1992: Chorology of trees and shrubs in south-west Asia and adjacent regions. **9**. — Institute of Dendrology, Polish Academy of Sciences, Kornik, Poland.

— 1993: Conspect and chorology of the genus *Pyrus* L. — Arb. Kornickie (Poland) **38:** 17-33.

Rehder, A. 1940: Manual of cultivated trees and shrubs, de. 2. — Reprinted 1987 by Dioscorides Press, Portland, Oregon.

Watkins, R. 1986: Apples (genus *Malus*); pears (genus *Pyrus*). — Pp. 187-196 in: Hora, B. (ed.), The Oxford encyclopaedia of trees of the World, ed. 2. Oxford. University Press, Oxford.

— 1995: Apple and pear. — Pp. 418-422 in: Smartt, J. & Simmonds, N. W. (ed.), Evolution of crop plants, ed. 2. — Longman, Harlow, U.K.

Way, R. D., Aldwinckle, H. S., Lamb, R. C., Rejman, A., Sansavini, S., Shen, T., Watkins, R., Westwood, M. N. & Yoshida, Y. 1991: Apples *(Malus)*. — Pp. 3-62 in: Moore, J. N. & Ballington, J. R. (ed.), Genetic resources of temperate fruit and nut crops, **1**. — Acta Hort. 290, ISHS, Wageningen.

Zagoja, S. W. 1983: Germplasm resources and exploration. — Pp. 3-10 in: Moore, J. N. & Janick, J. (ed.), Methods in fruit breeding. Purdue University Press, West Lafayette, Ind.

Zielinsky, Q. B. 1965: Self-incompatability of *Pyrus* species. — Bull. Torrey Bot. Club **92:** 219-220.

Zohary, D. & Hopf, M. 1993: Domestication of plants in the Old World, 2nd. ed. — Clarendon Press, Oxford.

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