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Origin and History of the Olive

Catherine Marie Breton, Peter Warnock and André Jean Bervillé

Additional information is available at the end of the chapter

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1. Introduction

To begin, the methodology followed to reconstruct the origin and history of the olive is presented. The genetic structure (density of alleles across the geographic distribution of individuals) based on allele frequencies of the present oleaster tree in the Mediterranean Basin computed with different methods of comparison with the genetic structure of cultivars grouped based on their geographic and genetic origins infers several possible scenarios for the transition from the oleaster to the olive. To screen among the scenarios requires solid dating in oleaster presence, diffusion and physical remains (from oleaster and cultivar trees) from different sites. Consequently, reconstructing the origin of the olive is based upon data from diverse disciplines and integrating them appears fruitful. Genetic data show that an event (such as bottleneck, migration, differentiation, adaptation) has occurred, but it cannot be dated. Thus it requires crossing genetic data with data gathered from different biological disciplines to make a strong case for this history. We examine successively:

1. The present distribution of the olive and its counterpart the wild olive,
2. Archaeological records of wood charcoals and artifact remains, ethno-botanical methods, pollen databases, and chemical methods for oil traces;
3. Molecular data obtained through 1995 to the present from *Olea europaea* and including relationships between varieties. We examined successively the evolution of methods to analyze data, the data sets examined through Bayesian methods, and the relationships between the oleaster and the olive in order to propose a wide scenario.

This article does not attempt to review all relevant literature on the history or background of the research, but rather focuses on the history of the olive tree and infers some shortcuts in the references of the work published. We apologize and readers can refer to recent general publications that fill the gap here [1, 2, 3, 4].

2. Dogma on the olive tree history

Domestication is based upon conscious behavior by humans over several centuries aimed at selecting among a species natural diversity those individuals that satisfied human requirements [5] such as in yield (seeds or other organs), composition (sugar, starch, fats, ...), and to harvest and maintain the cultivation of said species (seed attachment to spike or capitulum, dormancy of seeds, ...).

“However, human practices have had effects on the plant genome other than those intended through the conscious behavior of human domestication, effects which are highly documented for many crop species, especially cereals [6] barley, maize [7] Maize, [8] sunflower [9, 10], as examples.”

For wheat and grains which were weeds in wheat fields, the main domestication center has been the Near-East in the Fertile-Crescent documented by [11, 12, 13]. Botanists have therefore inferred that the olive tree may have followed a similar history. The presence of *Olea cuspidata* in the Mountains of Iran suggested a relationship between this species and the olive (Figure 1). Initial molecular results have eliminated this hypothesis and definitively anchored the origin of the olive in the wild olive only [14, 15]. Relationships between the subspecies of *Olea europaea* are not addressed in this chapter.

Present populations of wild olive (called “oleaster”) have questioned researchers on their origins. In the East of the Mitterrand they were considered natural. The famous botanist Pelletier has written, “the motherland of the wild olive tree is Anatolia”, where numerous wild olive trees make up dense groves, and De Candolle opines that “olive was originated from Asia Minor and spread from Syria over to Greece via Anatolia” [16]. The Flora of the Mediterranean basin is split into eastern and western halves by a line between the Cyrenaica basin of Libya and the Adriatic sea [17, 18, 19, 20]. Effectively, Botanists believe that the oleaster was native to the eastern or oriental half, and once domesticated the olive was transported by humans in the western half, where it thrives as feral form. Thus, all oleaster trees in the western Mediterranean would be feral trees [21].

This supposition has been widely accepted on plenty of open commercial internet sites selling olive products. We believe that this assertion is false and will demonstrate that idea through the results given from various teams working on the olive (Italy, Spain, France, Portugal, Morocco, Tunisia, ...).

Using the first molecular markers, namely isozymes, [22] has shown genetic differences between the wild and the crop in the west, but the results did not support an exclusive crop origin in the East, although in many internet sites, such as wikipedia, there is quotation of [23] Wikipedia to sustain the theory.

Readers may therefore encounter confusing theories dealing with the olive history. A number of commercial sites favor the olive’s origin as belonging to the commercial site’s country, but this has no scientific support. According to some commercial sites, the motherland of the olive is the island of Crete, according to others Southern Caucasia, Iran,

the Atlas Mountains in North Africa, Lower Egypt, the Sudan or even Ethiopia. Further, The wild-olive is a tree of the maquis shrubland, itself in part the result of the long presence of mankind.” [24].

In the west of the Mediterranean basin they were considered today, as a result of natural hybridization and the very ancient domestication and extensive cultivation of the olive throughout the Mediterranean Basin, wild-looking feral forms of olive, called “oleasters”, constitute a complex of populations, potentially ranging from feral forms to the wild-olive. We believe that feral forms cannot be called “oleaster” due to their origin from the domesticated olive.

3. State of the art on the olive tree

The olive tree contributes in shaping landscapes and has deep importance in the agro-economy, including the industrial economies based upon its by-products. However, the wild olive thrives in most of the domesticated olive’s cultivation area and the wild olive’s contribution to landscapes is far from neglected even though its contribution to agro-economy is weak. One faces some confusion on their respective identification [25].

The olive tree is now used for oil and canned-fruit production, with minor use of the wood for handcrafts. The leaves are used in medicine as herb tea, due to mainly their high phenolic compound content as oleuropein and hydroxytyrosol, which are beneficial in nutrition and medicine (see chapter 15, this book). What was the first use of the olive tree that justified initial care to wild trees? This remains a question and we suggest some tracks. First, the use of the wood and oil as a fuel, since the wood burns green and further the oil produces little smoke, an great advantage in caves in comparison to using animal fats for light and to warm [26]. The spread of olive oil has been documented in the Bronze Age by the features and artifacts (stones, pottery) and later by the containers (aryballos and alabasters) of the perfume industry which used olive oil as a perfume base [27].

All European civilizations have tree symbols: Ash tree (Scandinavian), Sycomore (Egyptian), Plane tree (Sparta, Greece), Oak tree (for the Gauls, Druids, to harvest mistletoe), Pinus (Japanese), (For the Buddha, India) and for Adam and Eve, The olive tree is markedly present in all religions (Christian, Judaism, Islam) symbolizing peace, aging, longevity, rejuvenating, authority, ... and plenty of legends and stories are anchored in its history in Mediterranean cultures [28]. However, a primary feature of the olive is that olive oil may also be sacred and has many religious associations. Chrism (consecrated or anointing oil) is made of olive oil, usually includes balsam, and spices. There are many legends on the origins of the olive tree, and all started with the myth of a spontaneous (Athena) or a foreign origin, as Arbequina cv. (Museum Borges Blanca, Catalonia, Spain). Chrism is used for Blessed Sacrament, unction (anointing) oil for baptism, confirmations, Eucharist or communion, marriage, for doing penance, ordination of priests, and extreme unction or the last rites. If olive oil did exist during the Bronze Age, its exact purpose is not well known [27].



Figure 1. *Europaea* subsp. *cuspidata* x *O. e.* subsp. *europaea* grown in INRA nursery (Near Montpellier, France) See [33].© André Bervillé.

The area where the wild olive thrives is restricted in comparison to the area where the olive is presently grown. Indeed, one of the consequences of the 7,000 to 8,000 years of olive domestication was to spread the cultivated olive out of the biological area of the wild olive, whereas the wild olive did not spread (Figure 3). Indeed, the history of the domesticated olive is tightly linked to mankind and their trend to colonize all the environments, even harsh ones, in order to avoid conflicts with other populations.

It could appear simple to recognize an olive tree [29, 30, 31, 32]. However, out of orchards and in the ecological area of the wild olive, it is not so easy due to many tricks that could lead to confusion with a wild olive. Now, we have abandoned the idea to make the differences rational for all criteria retained (morphological, phenological, molecular) a continuous variation between the two forms is recorded. Consequently, we have to keep in mind that all a priori discrimination between the two forms is questionable and that their confusion does not bias the results exposed here.

Other chapters develop the taxonomy of *Olea* that naturally thrives over all continents except the Americas, and the species *Olea europaea* L. that spreads over Asia, Africa and Europa and is used for its fruit in the Mediterranean basin, but is used for wood charcoal in the mountains of India and Africa [33, 34].

From a scientific point of view the olive is an orphan species, that means there is no model plant surrounding the genus *Olea*. Although several thousand DNA sequences are deposited in databases, little is known from the *Olea* genome, which remains to be sequenced.



Figure 2. First plane: landscape of abandoned Medieval olive groves surrounded by stone walls returned to natural appearance (Near Montpeyrroux South of France). © Catherine Breton.

4. The present distribution of the olive and its counter partner the wild olive

At present the oleaster is native in the following regions, and we can consider that since the last ice age the distribution has not changed, due to agricultural development the oleaster has disappeared in the agro-ecosystem, but it has not declined in the natural ecosystem (Figure 2). It is not an endangered species [30]. The wild olive tree thrives along the Mediterranean coasts. It is genuine in Spain, continental France and Corsica, continental Italy, Sardinia and Sicily islands, Greece and Turkey with Cyprus Island, and in all the east and south Mediterranean countries (Jordan, Lebanon, Syria, Israel, Egypt (Sinai) and Libya, it is present in plant formations. In Tunisia, Algeria and Morocco (Moulay-Idriss, Cascade d'Ouzou, Morocco; Ichkheul, Tunisia) once other tree species have been eliminated it may thrive as dense populations but is not a colonizing species.

Its current dispersal depends upon the wild olive trees that survived after the last ice age in refugee populations. However, its spread during the middle-Pleniglacial (Late Pleistocene) before the ice age is based upon wood charcoal and pollen sequences [17, 29, 35, 36] and it was present both in the Levant and in Spain. Based on this evidence, the oleaster is also genuine in the west. During the Holocene it is noticeable that it spread quickly and became abundant or dominant [35]. From a botanical point of view, there is no difference between the oleaster in the east and in the west.

Moreover, [35] analyzed botanical data to clearly identify the oleaster's associated with other thermophilous trees (*Ceratonia*, *Lentiscus*, *Phillyrea*, *Rhamnus*...) in the Mediterranean climate zone in comparison to those of the Atlantic formation (*Pinus*, *Betula*), which enabled them to define zones where the *Olea* has probably thrive.

However, the olive tree expanded widely outside the oleaster's limits and the famous French writer Georges [37] Duhamel has said "Là où l'olivier renonce, finit la Méditerranée" or 'There the olive has given up, the Mediterranean finishes', that means the olive tree is an excellent indicator of the Mediterranean climate. There is little knowledge on the spread of the olive, it was probably slow following the human colonization of harsh territories by populations seeking shelter to escape wars, and they were patient to adapt their cultivar set to the harsh environments. The spread of the olive follows the trade and settlement patterns of the Phoenicians from the Levant westward – to North Africa and Spain especially. Olive oil as both a trade good and utilitarian household item would have been a premier crop for any colonizer. The present diversity of the olive - probably around 2,000 cultivars - is a witness of this permanent fight between peoples and Nature [38]. The distribution of the olive tree around the Mediterranean basin goes in latitude northern and southern [39,40] and in elevation higher than the distribution of the oleaster tree (max 500m in Spain [31] (Figure 2).

The olive tree was introduced into the New World in South America by the Spanish (explorers and monks) at the beginning of the 1500's (Colombia, Peru, but later on the west coast of the USA). The common perception is that historic olive trees in California are dominated by the 'Mission' cultivar originally introduced by Spanish missionaries to the present day Caribbean and central Mexico in the early 1500's [41, 42]. Thomas Jefferson wrote to James Ronaldson on January 13, 1813, "it is now twenty-five years since I sent them (southern planters) two shipments of about 500 plants of the olive tree of Aix (Aix-en-Provence, France), the finest olive trees in the world." [43]. Olive seeds are believed to have been brought to California in 1769 to grow into trees hardy to 12 degrees Fahrenheit. Those olive trees were cultivated in the Franciscan Spanish monasteries. It was the Spanish who spread the olive to America. Catholic missionaries spread the olive to Mexico and later to California, as well as to South America. The late Earnest Mortensen of the Texas Agricultural Experiment Station brought olive trees to the Winter Garden area in the 1930's. It was introduced in South Africa after the Boer colonization and there it coexists with the subspecies *cuspidata*. In Australia the olive has been introduced by 1812 [21] and later cultivars were introduced in China, Japan, Argentina and Chili and in all countries with a

Mediterranean climate. When introduced as cuttings the cultivars were maintained, but when introduced as seeds unreferenced cultivars were obtained.

5. Archaeological records: wood charcoals, pollen sequences and artifact remains

The Oleaster

Due to oleaster wood being used as biofuel during the prehistoric age, abundant evidence exists to assess its presence from the pleniglacial to the Middle Holocene (for review see [35]). These authors stated that these kinds of remains constituted safe indicators for the presence of *Olea*, although endocarps and pollen grains may have accumulated due to human and wind transport them over undetermined distances.

The first record of olive wood is by [44] who found a fireplace dating to around 790,000 years ago containing (wild) olive wood charcoals. Wood-charcoal analyses carried out at prehistoric sites would reflect the local flora and therefore the frequency of *Olea* wood indicates its presence. Wood charcoals may be due to natural fires or from fireplaces in prehistoric sites depending on the sites and other remains in the site.

As reported by [35] the oldest site where *Olea europaea* thrived in Klissouva cave 1 (Southern Greece) which is dated to 61,140 – 55,230 Cal. Yr. BP. At Higueral de Valleja *Olea europaea* has been dated to 42,630 – 41,390 Cal. Yr. BP. *Olea europaea* has been present on both sides of the Mediterranean Basin, but obviously, such sites are scarcely distributed and do not allow us to draw an accurate map for the presence of *Olea europaea*.

Pollen sequences that contain Oleaceae family pollen may include pollen from *Phillyrea*, Jasmine (*Jasminum fruticans*), and Mediterranean ash tree (*Fraxinus angustifolia*) which thrives along rivers. The pollen is frequently transported long distances and accumulation sites (ponds, swamps, peat-lands) are often far from forests where the oleaster thrives. Thus some bias in pollen data may exist. However, pollen sequences are accurate for dating sites.

However, some of the oldest remains have been dated about to around one million years (wood charcoals from Israel [44] and leaf fragments from Tuff conglomerate [45]). Tuff does not give accurate aging of the site. These remains cannot attest to the presence of the actual oleaster, they belong to an *Olea europaea*, but the sub-species cannot be given. Moreover, such remains have been conserved due to exceptional favorable conditions and are too scarce to infer any model of distribution from them.

The Olive

When the oleaster first was tamed and received care marks the beginning of the domestication process. [29, 46] have shown that the wood charcoal kept traces of pruning practices because of specific vessel architecture and shape, as early as 7500 BP in the Portuguese Extremadura. Their results push back by 1,500 years the preceding estimation of olive domestication given in the eastern Mediterranean region.

Recently, Terral's team has revealed that wood charcoal could also reveals traces of watering in the Middle Ages [40]. If the reasons people were pruning the oleaster are unknown, the consequences of pruning probably appeared to these peoples by more regular blossoming over years and more fruits. Today olive cultivars display a wide variability in response to pruning methods that raises questions on the origin of the diversity [15, 47, 48, 49] at the Neolithic C site of Atlit-Yam on the Levantine coast (dated to 7100-6300 yrs. BP, uncalibrated C14) found underwater wells constructed of alternating layers of tree branches and stones, stone-installations, some lined with undressed stones and others dug into the clay sediment. Some of the crushing installations contained thousands of crushed olive-stones and waste resulting from the extraction of olive oil. So far this is the oldest known evidence for olive oil extraction.

Remains that enabled us to trace the olive tree are more and more numerous from the Mesolithic to the Historical periods. The most informative remains are olive endocarps (stones) that are frequently found in fireplaces (they are charred or carbonized). Terral's team has developed morphometric methods that appeared efficient in analyzing such remains [50]. The main features that result from their analyses are based on the fact that the morphometry of the endocarps has change during the domestication process. Using modern and ancient reference samples they screened and pointed out domesticated remains and unraveled some cultivar relationships. If many stones together in an archaeological site can reveal some transition phase between the wild to the domesticated olive (many broken stones together probably represent oil processing), numerous remains are single or a few stones and consequently these methods are limited on such samples. The accumulation of a few stones probably represents eating olives. However, secondary usage of olive pressing wastes may limit finding traces of olive oil production based on olive remains alone [51].

Pottery types absorb indications of the type of fat they have stored. Pottery types devoted to olive oil as containers for perfumes are aryballos and alabasters, which are widely present throughout the Mediterranean basin due to their diffusion by Greek and Roman cultures [52]. Ceramic chronologies are strict and factories are well recorded, providing a large corpus of data on exchange and trade during the historic periods. Documentation indicates that people used several plant oils (at least flax, saffron, safflower, castor oil and poppy), however, it is possible to differentiate plant oils from animal fats and to identify plant oils by the fatty acid composition obtained from pottery remains [53, 54, 55, 56].

Remains are concrete and their preservation is of importance for future diagnostic methods. The materials from sites studied by all the authors will probably tell more in the future. Furthermore, archaeology continues to uncover new sites and materials and this is likely to continue especially for the southern and eastern parts of the Mediterranean coasts.

In conclusion, the archaeological materials have enabled researchers from different disciplines to anchor the wild and cultivated olive in regions where they naturally thrived and colonized, respectively. Moreover, biologists and archaeologists have defined the basic elicit statistical differences between the wild and the cultivated olive for key historical

periods. All this information lays the foundation required to set up genetic models derived from the present genetic diversity recorded in the oleaster and in olive cultivars.

6. Molecular data enabling genetic inference for subsp. *europaea* in Mediterranean basin

All molecular data based on several types of methods (isozymes, RAPD, RFLP, ISSR and SSR) have been obtained since 1995 from *Olea europaea* [see 1-4 for review]. Obviously, we neglected reports that established relationships between cultivars unless they are informative in reconstituting the olive's history. Molecular data should be based on samples of wild trees and of cultivars representative of the present genetic diversity. If molecular data are bias in the sampling the conclusion will be probably biased. There is no *a priori* rational criterion for sampling oleaster and olive cultivar trees due to the ignorance of their origin. Several hundreds of publications have reported data based on different types of molecular markers on various samples of wild trees and cultivars (depending on the country, the easy sampling of wild trees (from the local region or covering several regions) and with different methods to analyze data.

Evolution of methods to get and to analyze molecular data

Evolution of methods is permanent due to progresses in their development. We will not reiterate all methods of studying the history of the olive since the last ice age through domestication, but will try to enable non geneticists to follow our reasoning. The progress in developing molecular markers over the last twenty years has made some techniques lapsed, although they have released plenty of information [4, 57].

Whatever the techniques used to visualize the genetic diversity, the main feature is to aggregate data from the three DNA supports in the olive tree: the mitochondrial DNA (mt,), the Chloroplast DNA (cp, [58] and the nuclear DNA (nu-, [15, 59, 60, 61]. The information brought by the three compartments is not proportional to the length of the DNA, but by the mode of inheritance and by their mode of evolution. The mt-DNA is maternally inherited as the cp-DNA [62], and evolves by recombination and by mutation and deletion, respectively. These DNA pools are constituted from several copies of the same molecule (they are haploid) and define 'haplotype'. The nuclear DNA is made of two halves from each parent. If the two alleles at one locus are discernible they are said to be codominant, and if only one is discernible due to the other one being absent then the discernible allele is dominant over the hinted allele. If the same dominant allele is found in two different individuals they are said to be similar, whereas if the same two alleles are found in two different individuals they are said to be identical.

Population genetic methods based on similarities (established for dominant alleles) compares at each locus two heterogeneous groups, one homogenous (the double recessive) and one heterogeneous (the double dominant and the heterozygous). All methods used to structure the genetic diversity are based on the allelic frequencies that are firm with co-

dominant markers but are estimated with dominant markers, i.e., Correspondence (FCA) and Hierarchic analyses (leading to dendrograms). Bayesian methods for nuclear DNA (nu-DNA) appeared in 2000 to analyze the data sets and they enable to constitute clusters (based on inferences of allele frequencies) and to check in each individual under examination the proportion of the genome that is coming from the different groups made by the software [63]. These clusters under some hypotheses may correspond to ancestor origins. However, Bayesian method can mix data from nu-, and cp- or mt-DNA. All the methods have contributed in eliciting the olive's origin and they have opened the way to use more adequate methods [64]. Obviously, old data sets could be treated with new methods to get new information.

By the year 2000, after several completed projects (European projects and country projects), the molecular diversity in the wild form appeared deeply structured, that means the geographic distribution of the molecular markers in the wild tree was not homogenous [1, 24, 65, 66]. The genetic structure (estimated by the F_{st}) was stronger with mt- and cp-DNA markers than with the nu-DNA. Moreover, the mt- and cp-DNA distribution in the eastern and the western halves of the Mediterranean Sea appeared strongly structured. Even if sampling problems for all the studies had biased their data, the trend from the whole data supports that clines for allele frequencies do exist in the wild olive diversity. The clines could be due to different causes and as for other tree species the spread of the wild olive at the end of the last ice age may explain its present distribution.

Data sets examined

All data on the olive and oleaster can be analyzed as i) botanical samples to look for a key to differentiate them ;ii) similarity records to try to differentiate the two forms from a statistical point of view, and iii) genetic relationships using Bayesian methods.

The botanical differentiation between the oleaster and the olive, although with numerous attempts, does not reveal key traits neither morphologic nor molecular [31, 47, 67].

Similarity records have been shown more effective in differentiating between the two forms. Clear cut separation has occurred though some trees remained not clustered, which may indicate that there are hybrid forms between trees from the two groups or that all trees did not share all the traits recorded either morphological or molecular. Low frequency markers should be eliminated in such analyses as they may weigh too much and may distort the results. These methods lead to references of phylogenetic relationships between different levels of taxa, even though, they are not accurate for distant taxa (species, genera), but they have shed light on variety relationships for the olive [47, 64, 68, 69].

[57] Breton has examined a wide sampling of about 1900 trees including wild olives (950 from 55 sites), old trees (50) with undetermined status, and cultivars (about 900, either abandoned, feral forms or from collections) sampled in most places around the Mediterranean basin (Figure 3). Using 16 nu-DNA loci (Single Sequence Repeat or SSR) and 3 cp-DNA loci (single base repeats), the comprehensive data set was examined using

structure software [63] by different a priori packages made of oleaster trees, cultivars, oleaster and feral trees. All clusters revealed by this study were checked by other aggregation methods (FCA, Dendrograms) to verify their consistency. However, these methods cannot ensure the biological existence of such groups. [70] have examined about 250 cultivars and two oleaster populations with AFLP markers (there are mostly dominant markers) from the central Mediterranean with similar methods. [71] has examined 171 wild trees with 8 SSR from the north-western Mediterranean [30] has studied about 32 cultivars and 70 oleaster trees from Tunisia, with morphological and molecular methods.



Figure 3. Anti Atlas Morocco elevation 1525masl. © Catherine Breton

7. Relationships between the oleaster and the olive

[70] Baldoni et al. concluded that most cultivars have been introduced into Central Italy regions from the outside and that Umbrian cultivars have originated by selection from local oleaster trees.[71] Belaj et al. concluded that the genetic structure (=density of alleles across the geographic distribution of individuals) is not strong enough to positively establish relationships between true oleaster trees and cultivated varieties. The impact of these studies has probably been limited due to the limited sampling of the wild forms. [30] Hannachi et al. (2009) has revealed that the cultivar sets can be split into those of local

origins and those introduced from the Near-East and western regions, making Tunisia in central Mediterranean a key-place for olive and oleaster diversity. [57] Breton concluded that the oleaster populations were structured in at least eleven ancestral populations, which colonized the Mediterranean basin after the last ice age, following mostly the sea-coasts. Based on coincidence of the sampling area and the clusters, some geographic zones for the refugee populations have been suggested: 1) Four in the East (Turkey, Cyprus (2) and Israel+ Lebanon), 2) four in the central Mediterranean (including North of Africa, and main islands Sicily, Sardinia, and Corsica) and 3) three in the western Mediterranean (Continental Spain (2) and South France). The zones were well defined in the East and wide in the West, probably due to limited sampling in Spain and continental Italy.

Crossing models based on historic methods and genetic based-hypotheses

[57] Breton applied the same methods to the cultivar set. Although other methods could not split the cultivars into different groups based on biological criteria [47], nine clusters were clearly defined. Furthermore, domestication centers have been revealed by crossing the oleaster and cultivar clusters. Nine domestication centers appeared. The main features from all these results are that the genetics suggests clusters and relationships that remain obscure without data to confirm them. Coincidences between the pre-domestication evidence in Portuguese Extremadura [29] and one refugee zone in central Spain [57] strengthen each other. Carrión et al. points out that the accurate records of all archaeological sites where the oleaster or the olive was found sustains some other sites in the west (Spain, see fig. 3 in [35]) and in the east (Cyprus).

Using the same methods (Wide sampling, Bayesian clustering, FCA and dendrograms) [64] have shown that by admixture analyses for some olive cultivars it is feasible to attribute different origins in the glacial refugees and furthermore the proportion of each origin is quantitatively computed by the Structure software. The application of this method to cultivars will enable us to have a clear view of the cultivars' origins. Data supports that in a western country most cultivars have been introduced from the eastern Mediterranean, but that some cultivars have their origin in local oleaster [72] Ozkaya. [30] Hannachi et al. used this method to reveal three olive origins in Tunisia from the north of Africa (Maghreb), the Near-East, and the west (Spain).

Archaeological remains could release more information by studying the DNA for other species. The method has been applied successfully to olive stones [73]. Many olive remains could be analyzed, but the method is still risky. Today, all these data converge to sustain that in each region the present olive cultivar diversity is either or both the result of ancient introductions from the Near-East and/or from other area (North of Africa, Cyprus, Turkey), local selection from oleaster trees, and from crosses between oleaster and ancient cultivar trees. More details on the history of the oleaster tree could be obtained at local levels and with reference to sampling the whole Mediterranean. Dialogue between researchers from the different fields will be required.

All these data converge to sustain that in each region the present olive cultivar diversity is either or both the result of ancient introductions from the Near-East and/or from other area (North of Africa, Cyprus, Turkey), local selection from oleaster trees and from crosses between oleaster and ancient cultivar trees. However, the self-incompatibility system in the wild olive and the olive is still not yet known, leaving the selection pressures that occurred along the domestication processes unknown, which are required to gather enough S-alleles in a region to enable fruit set. [74] Breton & Bervillé have recently deciphered S-allele pair wise combinations for a few varieties, and it appeared which varieties may combine efficiently, at least *in silico*, but it remains to experimentally check coincidence in blossoming and other compatibility levels, which may affect development of pulp and embryo. The model developed infers which genotypes may coexist to ensure correct fruit set, even though self-compatibility appears inherent to most varieties.



Figure 4. Abandoned olive trees along the Mediterranean coast (North of Catalogna, Spain)
© Catherine Breton

8. Conclusion

The origin of the olive tree displays singularities in comparison with other tree species. As well detailed by [35] the thermophilous requirements of the oleaster has constrained its diffusion. The domestication process has spread out the crop into harsh environments (in northern latitude, deserts, higher altitude) creating plenty of cultivars. About ten domestication centers may be at the origin of this diversity for adaptation to these environments. Recent findings in olive S-allele relationships have not been taken into account here to show the olive's history. The mode of reproduction of the species has probably played a major role enabling self-progenies and thus narrow local adaptation, thus explaining logically the huge diversification encountered in this species.

Author details

Catherine Marie Breton

Present address: CNRS ISE-M UMR 5554, Montpellier, France

Address: INRA , TGU AGAP, Equipe DAVEM, Montpellier, France

Peter Warnock

Missouri Valley College, USA

André Jean Bervillé

INRA, UMR DIAPC, Montpellier, France

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