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Debate / Débats

The origins of the domestication of the olive tree

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Abstract

The present diversity of the olive (crop) and oleaster (wild) tree was investigated with nuclear and cytoplasm markers. Patterns of diversity of the wild form inferred eleven ancestral populations in the East and the West of the Mediterranean basin. Patterns of diversity for cultivars are less clear, but we showed that cultivars admixed to nine groups that corresponded to oleaster ancestral populations. We inferred that nine domestication events took place in the olive, but these origins were blurred by gene flow from oleaster and by human displacements. These origins of domestication probably reflected different reasons and uses to domesticate the oleaster. ***To cite this article: C. Breton et al., C. R. Biologies 332 (2009).***

Résumé

Les origines de domestication pour l'olivier. La diversité actuelle de l'olivier (cultivé) et de l'oléastre (sauvage) a été étudiée avec des marqueurs nucléaires et cytoplasmiques. Les patrons de diversité de la forme sauvage conduisent onze populations ancestrales à l'Est et l'Ouest du bassin méditerranéen. Pour les cultivars, les patrons de diversité sont moins tranchés, mais nous avons montré qu'ils se rattachent à neuf groupes qui correspondent à neuf des onze populations ancestrales d'oléastre. Nous en avons déduit que neuf évènements de domestication différents se sont produits pour conduire à l'olivier actuel, mais les origines sont rendues diffuses du fait de flux de gènes avec l'oléastre et des déplacements des cultivars par l'homme. Ces origines de domestication reflètent probablement diverses motivations et utilisations de l'olivier et de ses produits. ***Pour citer cet article : C. Breton et al., C. R. Biologies 332 (2009).***

Keywords: Domestication centre; Gene flow; Olive tree; Oil; Refuge zone

Mots-clés : Centre de domestication ; Flux de gènes ; Huile ; Olivier ; Zone refuge

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The olive is the most emblematic tree of the Mediterranean basin [1]. Its domestication is considered to have occurred in the Near-East [2] and it spread further from the East to the West of the Mediterranean basin with human migrations [3,4]. The introduction of the olive by the Greeks in Marseille 2500 years ago, is well documented everywhere [3,4], and, although the oleaster and the olive were already present, the Greeks probably introduced new olive cultivation methods. Recent molecular studies have brought information on the oleaster life history since the last Ice Age [5] as well as on cultivar relationships. Several domestication events have probably occurred for this species as demonstrated by the diversity of cultivars based on chlorotypes; thus genetics may recognize them, but the chronology of the events should be based on archaeology remains [6]. Consequently, the olive domestication origin is controversial, and should be revisited as should the hypothesis that the olive has been introduced into the West from the East of the Mediterranean basin. Olive cultivars display huge diversity. The question is whether they differentiate after domestication or if they have several origins.

The olive is the cultivated form, whereas the oleaster is the wild form of *Olea europaea* subsp. *europaea* [7]. They are called var. *europaea* and var. *sylvestris*, respectively [8]. The crop is propagated either by cuttings or grafts and therefore cultivars are clones. The transition between the oleaster and the olive is based on the size of the pit remains in artefact records. Nevertheless, they are more than 2000 cultivars in the Mediterranean basin that displays huge diversity based on fruit morphology and pit size and morphology and several modern cultivars display as small pits as the oleaster, making the distinction criteria doubtful [9].

Be that as it may, the olive is considered as having been domesticated during the early Neolithic in the Near-East, based on archaeological remains [10]. Several authors underlined the need to cross genetics with archaeology to unravel domestication origins [11]. Traces of olive exploitation have been recorded in the Portugal–Spain Extremadura [12,13], suggesting an early domestication in this region.

Domestication from a wild species to a crop has occurred usually once in the life history of most species [11]. However, for rice and cereals, two or more events have been recorded [14,15]. The crop usually displays a bottleneck of diversity in comparison to the wild due to genetic drift. However, genes under selection are not yet identified for the olive due to a gap in knowledge of the reasons why people have domesticated it. Probably its fruits were used directly, thus leading to increase fruit size. However, we have no evidence whether fruits were used for cakes or oil. It is not obvious that the oleaster was domesticated for its oil. It is logic to think that pickling of the olive wood – since it burns even when wet and was used for feeding animals – has led to domesticate the olive for its fruits [16]. Olive oil uses are numerous and the first uses were probably shamanistic and to burn oil in lamps. The advantage of olive oil is that it burns without smoke; the feed use is documented later, during the Bronze age [17].

Recently, molecular marker studies, both nuclear and cytoplasmic, have revealed that oleasters survived the last Ice Age in eleven refugees [6,18]. Surprisingly, the refugees are less numerous in the East (two in Turkey + Cyprus and Palestine), than in the central Mediterranean (five in Corsica, France; Tunisia) and in the West (four in Morocco, Algeria; Spain, and France). The role Tunisia plays in the central Mediterranean has never been suspected for the oleaster [18]. Nevertheless, the chlorotype genetic structure did not fit with the refugees. The main genetic structure difference shown is based on chloroplast DNA polymorphisms (Fig. 1, A, B) from about 1500 trees [18]. We have found the chlorotype CE1 almost unique in the East (Continent, and Greek Islands), except in Cyprus where it spread with the chlorotype CE2, whereas in the West the major chlorotypes are CE1 COM with two variants (COM1 and COM2) for Spain and the main islands (Sicily, Sardinia, Corsica and the Balearic islands) and the chlorotype CCK mainly in the North of Africa; this suggests that the chlorotype came from ancestral *Olea europaea* subsp. and were assimilated into the oleaster by introgressive hybridization before the last Ice Age [19]. CE1 is present everywhere. Probably, this genetic structure is the result of gene flow from cultivars displaced by humans and with the wild olive [7,20].

Gene flow is indicated by the reduced natural spread of the wild olive in comparison to the spread of the cultivars by humans. The spread of the wild is limited to the Mediterranean basin, whereas the cultivars spread in sub-desert regions (South of Tunisia, Morocco, and Libya) and to mountains (Lebanon, Greece, Italy, Spain, France, Portugal) where the oleaster cannot survive alone. Recently, humans have moved the olive tree to all countries with a Mediterranean climate (Africa, Australia, Asia, and America) [1].

Moreover, several approaches have failed to reveal a clear genetic structure in olive cultivars based on different molecular markers, and indeed, olive uses. Based on several types of molecular markers cultivars form a compact genetic group difficult to split based on olive uses, fruit morphology, cultivar locations and on their