



Systematics, ecology and phylogeographic significance of *Olea europaea* L. ssp. *maroccana* (Greuter & Burdet) P. Vargas *et al.*, a relictual olive tree in south-west Morocco

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Within the genus *Olea*, the olive (*Olea europaea* L.) possesses the largest geographic distribution, and several sub-species have been described. South-west Morocco harbours an endemic olive, *O. europaea* ssp. *maroccana* (Greuter & Burdet) P. Vargas *et al.*, located in the western part of the High Atlas (mainly on the southern slope of the Ida-ou-Tanane massif) and in the western Anti Atlas. The existence and the taxonomic position of this tree have long remained uncertain, but the combination of several morphological traits is unique. Nuclear and cytoplasmic DNA polymorphism also demonstrate that this tree is a well-differentiated and relictual taxon, probably originating from an ancestral unit within tropical Africa. Our findings refute the opinions of several authors who consider ssp. *maroccana* to be intermediate between the cultivated olive (*O. europaea* ssp. *europaea*) and the Saharan olive (*O. europaea* ssp. *laperrinei* (Batt. & Trab.) Cif.). According to cpDNA and mtDNA analysis, the Moroccan olive and the Canarian olive (*O. europaea* ssp. *guanchica* P. Vargas *et al.*) are related and belong to the same sub-taxon. This biogeographical affinity is strongly supported by other recent phylogenetic studies. The long-term viability of ssp. *maroccana* is threatened by several factors: (1) limited distribution and reduced numbers of individuals within isolated populations, (2) fragmentation processes related to human and livestock pressures, and (3) putative gene flow between this taxon and the cultivated olive. In order to ensure the long-term survival of this endemic olive, a specific program of conservation should be implemented in the near future.

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INTRODUCTION

The genus *Olea* (Oleaceae) contains approximately 40 species and sub-species, extant throughout Africa, Europe, Asia and Oceania (Green & Wickens, 1989; Besnard, Green & Bervillé, 2001); the olive (*Olea europaea* L. s.l.) is the species with the widest distribution. Green & Wickens (1989) recognized several olive sub-species, including *Olea europaea* ssp. *europaea*, one of the oldest cultivated trees within the

Mediterranean Basin (Zohary & Spiegel-Roy, 1975). Recently, another olive has been described in Morocco (Barbero *et al.*, 1982), *Olea maroccana* Greuter & Burdet. Despite its taxonomic, ecological and phyto-geographic significance, this taxon remains poorly known.

The presence of an olive specific to the western High Atlas (particularly on the Ida-ou-Tanane massif) was suspected by Jahandiez & Maire (1934) after its first collection by Maire in 1922. They described the olive trees of this region as having long, narrow, and sharp leaves, and considered them as morphologically similar to *O. europaea* ssp. *laperrinei* (Batt. & Trab.) Cif.

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from the Saharan mountains. Since then, a number of observations have sustained this opinion (C. Sauvage, Schoenenberger, pers. comm.), although Maire (1933) indicated that the Moroccan olive was distinct from the Saharan populations. He stressed that the former possesses an inflorescence inserted on short axillary branches with one or two pairs of folioles.

Nevertheless, no complete herbarium sample of the Moroccan olive had been collected, and flowers and fruits had not been described. Consequently, the taxonomic status of this tree remained unknown. In 1980, as part of an investigation of the plant communities of the argan [*Argania spinosa* (L.) Skeels] area in south-west Morocco (Barbero *et al.*, 1982), more detailed observations confirmed that a distinct tree existed in sympatry with *O. europaea* ssp. *europaea*. This taxon was described in a marginal note by Barbero *et al.* (1982), and named *Olea salicifolia* Barbero, Benabid, Quézel, Rivas-Martinez & Santos. However, because this name was already attributed to an Indian species (*O. salicifolia* G. Don. fil. 1837), it was renamed *O. maroccana* Greuter & Burdet (Greuter & Burdet, 1989). Following our morphological, molecular and phylogeographic investigations (see below), and those of other workers (Hess, Kadereit & Vargas, 2000; Vargas *et al.*, 2001), we suggest that this olive tree is more accurately ranked as *O. europaea* ssp. *maroccana* (Greuter & Burdet) P. Vargas, J. Hess, Muñoz Garm. & Kadereit.

Since its description in 1982, this endemic Moroccan olive has been observed and collected by a number of botanists. Its distribution has become better known as it has also been found in the western Anti Atlas (Benabid & Cuzin, 1997). Moreover, recent molecular studies of the Mediterranean *Olea* (Besnard & Bervillé, 2000; Besnard Green & Bervillé, 2001) have shown that *O. europaea* ssp. *maroccana* is characterized by its own set of specific traits. Local communities (of the Souss valley) also clearly distinguish these two olive species, as they do not consume the fruits of the endemic olive. Nevertheless, no study has been devoted to this tree which constitutes a noteworthy Moroccan endemic, of very exiguous distribution and whose conservation remains uncertain.

The objectives of our study were as follows:

- (1) Specify the taxonomic identity and the systematic position of the Moroccan olive with respect to the other olive taxa belonging to the *O. europaea* complex (notably *O. europaea* ssp. *laperrinei*, *O. europaea* ssp. *guanchica* P. Vargas, J. Hess, Muñoz Garm. & Kadereit, and *O. europaea* ssp. *cerasiformis* (Webb & Berth.) Kunkel & Sunding), using morphological characters and molecular markers.
- (2) Define its ecology and the chorology of this Moroccan endemic.

- (3) Determine the biogeographic context within which the species has differentiated.
- (4) Assess the threats to populations and propose steps for sustainable conservation.

TAXONOMIC ELEMENTS OF THE *OLEA EUROPAEA* COMPLEX

The complicated and controversial taxonomy of the *O. europaea* complex will be discussed only insofar as it is relevant to the understanding of ssp. *maroccana*. The taxa belonging to this complex constitute a relatively homogeneous unit, and we follow the taxonomic proposals of Green & Wickens (1989) amended by Vargas *et al.* (2001), although the taxonomic key the former provide is quite difficult to use. In fact, as suggested by Hess *et al.* (2000), there is a discrepancy between the actual taxonomy of the *O. europaea* complex and a more natural classification which includes phylogeographic data.

This complex is extant in the Mediterranean Basin, in tropical and temperate Africa, and in temperate and sub-tropical Asia (Green & Wickens, 1989; Besnard, Green & Bervillé, 2001). The subspecies with the largest distribution, ranging from southern Africa to southern China, is *O. europaea* ssp. *cuspidata* (Wall. ex G. Don) Cif., for which several taxa have been described: *O. africana* Mill. (= *O. indica* Kleinhof ex Burm. F.) from the Cape to the banks of the Red Sea, *O. chrysophylla* Lam. in eastern Africa and southern Arabia, and *O. cuspidata* Wall. ex G. Don from Iran to the Himalayas. In temperate regions, the other olive taxa are (Fig. 1):

- (1) *O. europaea* ssp. *europaea*, extant in the Mediterranean Basin, which groups the wild Mediterranean olive [oleaster = var. *sylvestris* (Miller) Lehr.] and cultivated forms (var. *europaea*).
- (2) *O. europaea* ssp. *guanchica*, endemic to Canary Islands.
- (3) *O. europaea* ssp. *cerasiformis*, endemic to the three islands of Madeira (Press & Short, 1994), already considered as a subspecies by Hansen & Sunding (1993), and recently highlighted by Hess *et al.* (2000) and Vargas *et al.* (2001).
- (4) *O. europaea* ssp. *laperrinei*, extant in the mountains in central-southern Sahara and eastern Sahel.
- (5) The olive tree restricted to south-west Morocco (formally named *O. maroccana*), whose taxonomic position is uncertain.

Chevalier (1948) believed that the Moroccan, Macaronesian and Saharan olive trees had to be grouped into an unique entity, *O. chrysophylla* Lam. var. *maderensis* (Lowe) A. Cheval. Sauvage & Vindt (1952) considered the endemic Moroccan olive as intermediary

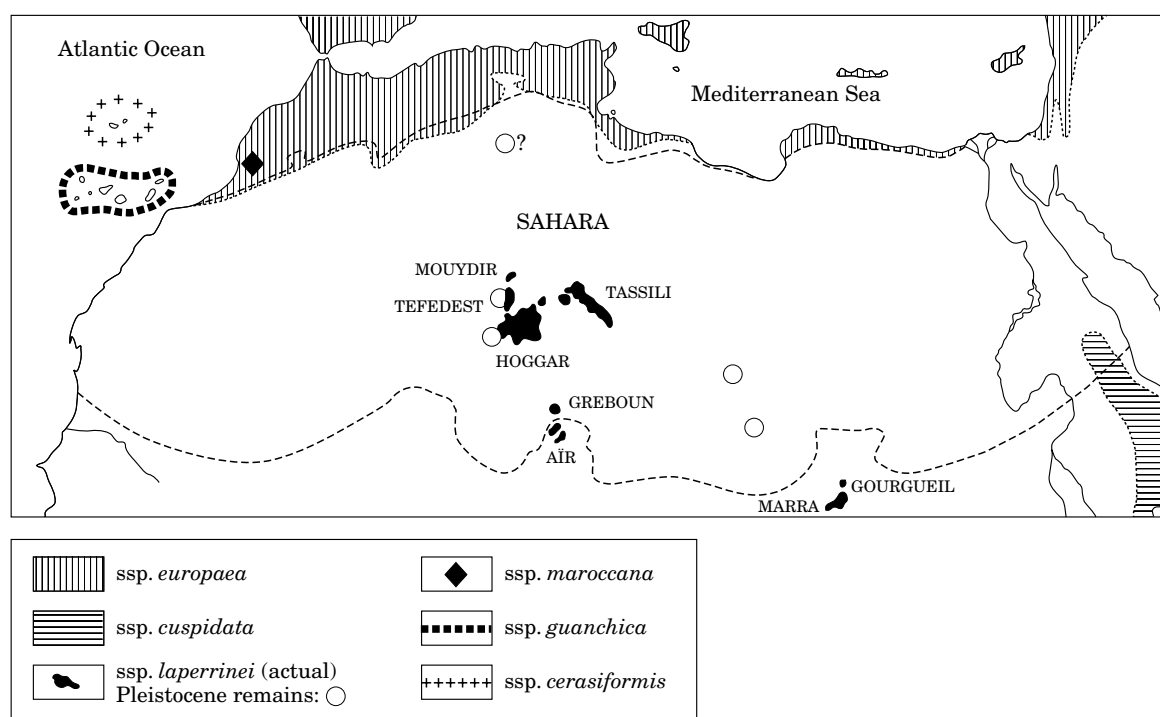


Figure 1. Distribution of the taxa of the *Olea europaea* complex (adapted from Quézel, 1962, 1978). (---) limits of the Sahara.

Table 1. Mean and standard deviations of the three leaf characters considered for the five taxa of the *Olea europaea* complex

	Length	Width	Length/width	No. individuals examined
<i>ssp. guanchica</i>	51.55 ± 11.07	8.88 ± 1.81	6.01 ± 1.63	17
<i>ssp. europaea</i>	44.55 ± 9.1	10.75 ± 3.14	4.33 ± 0.9	11
<i>ssp. laperrinei</i>	51.05 ± 5.7	5.93 ± 0.81	8.65 ± 0.17	4
<i>ssp. maroccana</i>	52.49 ± 10.96	7.19 ± 1.85	7.54 ± 1.68	11
<i>ssp. cerasiformis</i>	58.07 ± 20.98	8.04 ± 1.37	7.26 ± 2.34	10
All groups	51.48 ± 13.17	8.53 ± 2.44	6.41 ± 2.06	53

between *ssp. europaea* and *laperrinei*, whereas Green & Wickens (1989), Zohary & Hopf (2000), Hess *et al.* (2000), and Amane *et al.* (2000) included it in *ssp. laperrinei*.

MORPHOLOGICAL DESCRIPTION OF *OLEA EUROPAEA* SSP. *MAROCCANA*

Our descriptions are based on measurements or observations of morphological traits, complemented by data from Benichou (1962), Green & Wickens (1989) and Press & Short (1994).

Differences in leaf morphology between 53 individuals belonging to the five Mediterranean and Macaronesian taxa of the *Olea europaea* complex were examined for three characters (length, width, length/width ratio). Means and standard deviations are indicated in Table 1. MANOVA (Statsoft, 1997) was

performed to test the differences between taxa. The normality of the distributions was visually checked using a normal quantile plot, and the homogeneity of the variances was tested using the Levene test ($P < 0.05$ for each variable). The results indicate that the differences are highly significant when we consider all the species (Wilks' lambda : 0.4363, $P = 8.10 \cdot 10^{-6}$, $df = 12$), but only the width and the ratio length/width are significantly different (Table 2). A subsequent multiple post-hoc comparison was performed by a Tukey test for unequal sample sizes (Statsoft, 1997), in order to assess the differences between pairs of species. Significant differences were obtained only between *ssp. maroccana* and *europaea* for both width and length/width ratio (respectively $P < 0.0018$ and $P < 0.0004$).

Due to the lack of mature individuals of *ssp. maroccana*, generally cut by the local inhabitants, the

Table 2. Results of the MANOVA related to the three leaf characters considered for the five taxa of the *Olea europaea* complex

	Mean square effect	Mean square error	F (df 1.2)	P
Length	243.4795	167.6435	1.4523	0.2314
Width	26.3251	4.2558	6.1856	0.0004
Length/width	22.9154	2.6666	8.5933	0.0002

description below is based on approximately 20-year-old shoots from stumps.

HABIT: arborescent or shrubby, evergreen, 4–5 m high, generally pluricaulous, branches and ramifications erect, internodes of terminal ramifications elongate, reaching 20–60 mm. **BARK:** smooth, grey-brown. **LEAVES:** lanceolate to lanceolate-acute, (30)40–70(80) × (4)6–12(13) mm, slightly contracted into an acuminate reddish-brown apex and progressively contracted into a medium petiole (2–7 mm); lateral nerves not visible or scarcely visible, principal nerve partly canaliculate on the lower side, leaf-blades with revolute margin; glossy dark-green and very sparsely scattered with tectorous and star-like hairs above; whitish and densely covered by flattened tectorous hairs beneath. **INFLORESCENCE:** flower-bearing panicles axillary and terminal, elongate and flexuous; lateral ramets 50–70 mm long, ramified; secondary ramets 10–30 mm long; terminal ramets reflected, 60–120 mm; inflorescence bracts lanceolate-obtuse, 3–4 mm long. **FLOWERS:** rather large, 4–6 mm in diameter, white-yellowish; inferior flowers pedunculate (2–4 mm) with 2 bracteoles ovoid-elongate of 1–2 mm and inserted either on the pedicel or beneath the calyx; calyx urceolate, erect, cylindrical-oval, c. 1 mm long. **FRUIT:** globose-ovoid drupe, 9–11 × 5–7 mm, obtuse at the apex, green then red-brown when unripe, becoming purplish-black; pulp carmine and aqueous, sweet or slightly bitter taste.

O. europaea ssp. *maroccana* possesses some distinct morphological characters in comparison with the other taxa of the *O. europaea* complex (Table 3). It is close to ssp. *laperrinei*, based on leaf characters, fruit, and the inferior flower (Benichou, 1962). Leaf dimensions of the Moroccan olive are more homogeneous than those of ssp. *cerasiformis* and *guanchica*, whereas it has more linear leaves than ssp. *europaea*. It is the only taxon with partly canaliculate nerves on the abaxial side. The most important morphological character is the presence of well developed bracteoles on the floral pedicel for ssp. *maroccana*, *cerasiformis* and *cuspidata*, but not for ssp. *europaea* and *guanchica*. The sweet or slightly bitter taste of ssp. *maroccana* is also a practical distinctive character with regards to the putative sympatric ssp. *europaea*.

MOLECULAR CHARACTERIZATION OF *OLEA EUROPAEA* SSP. *MAROCCANA*

The samples used for the molecular study are listed in Table 4. First, these individuals were characterized by chloroplast DNA (cpDNA) and mitochondrial DNA (mtDNA) polymorphism using PCR and RFLP methods respectively (Besnard *et al.*, 2000, in prep.). These organelle DNAs are maternally inherited in olive (Besnard, Green & Bervillé, 2001), and a high genetic disequilibrium linkage between cpDNA and mtDNA polymorphisms has been detected (Besnard *et al.*, in prep.).

The cpDNA phylogenetic tree supports the existence of five clusters corresponding to distinct geographic zones (Fig. 2; Besnard *et al.*, in prep.): *C* in Asia, *A* from Kenya to South Africa, *E1* and *E2* in Saharan Africa and the Mediterranean Basin, and *M* in the Macaronesian Islands and south-west Morocco, in which ssp. *maroccana* is included. Based on these data, ssp. *maroccana* and *guanchica* are very closely related, although they display a relatively high haplotype diversity (Table 4). Here, we present an additional analysis based on mitochondrial polymorphism. Six mitochondrial variants (mitotypes) have been recognized in the Mediterranean Basin (Besnard *et al.*, in prep.). We constructed a presence/absence matrix of RFLP mitochondrial fragments. Using Nei & Li distances (Nei & Li, 1979) and the Neighbor Joining algorithm (Nei, 1987), a phenetic tree was constructed to represent the genetic relationships between the six mitotypes. To construct this tree, we used a non-redundant binary matrix (redundancies resulting from an equivalent pattern revealed by the same probe for different restriction enzymes). In order to check the reliability of tree topologies, one thousand bootstraps were performed (Felsenstein, 1989).

Furthermore, we used available RAPD information (Besnard *et al.*, 2001) to compare different taxa with ssp. *maroccana*. Seventy-nine markers revealed with eight primers (decamers: A1, A2, A9, A10, C9, C15, E15, and O8) were used. A binary presence/absence matrix for each fragment was constructed for all individuals. We performed a correspondence analysis using the CORRESP procedure of SAS (SAS Institute, 1992).

Table 3. Morphological characters of *Olea europaea* ssp. *maroccana* in comparison with the other taxa of the *Olea europaea* complex. Qualitative data for (A) general appearance and leaves; (B) flower and fruit traits

		General appearance						
		Leaves						
Subspecies of the <i>Olea europaea</i> complex	Height of the tree	Trunk	Shape	Colour	Apex	Length (cm)	Width (cm)	Petiole length (cm)
<i>maroccana</i>	1-4(5) m	Pluricaulous, smooth grey-brownish	Lanceolate to linear	Dark-green above, whitish beneath	Acuminate to mucronate	(3)4-7(8)	(0.4)0.6-1.1(1.3)	0.2-0.7
<i>europaea</i>	1-15 m	Monocaulous or pluricaulous, grey	Lanceolate to obovate	Dark greyish-green above, light grey beneath	Mucronate	(2)5-6(8)	(0.5)1-1.5(2)	0.3-0.6
<i>guanchica</i>	1-6 m	Pluricaulous, grey or whitish	Oblanceolate to elliptic	Greyish-brown above, paler beneath	Mucronate to cuspidate	(2)3-7(8)	(0.4)0.6-1.1(2.1)	0.2-0.5
<i>cerasiiformis</i>	1-2.5 m	Pluricaulous, grey or whitish	Oblanceolate to linear, rarely suborbicular	Greyish-green above, paler beneath	Acuminate to mucronate	(3)4-8(10)	(0.4)0.6-1(1.4)	0.3-0.7
<i>laperrinei</i>	1.5-3(5) m	Mainly monocaulous	Lanceolate-linear to linear	Ashy-green above, whitish-silvery beneath	Clearly mucronate	(2.8)4-5(7)	(0.3)0.5-1(1.5)	0.2-0.4
<i>cuspidata</i>	3-14 m	Mainly pluricaulous, dark brown, rough	Narrowly-lanceolate to ovate	Silvery or reddish beneath	Obtuse or mucronate	(3)5-6(9)	(0.5)1-1.5(3)	0.3-0.8
(B)		Drupes						
		Flowers		Bracteoles of the floral pedicel		Shape		Pulp colour and taste
Subspecies of the <i>Olea europaea</i> complex	Panicles (cm)	Colour	Corolla diameter (cm)	Well developed	Missing	Dimensions (cm)	Shape	Pulp colour and taste
<i>maroccana</i>	5-7	Yellow-whitish	0.4-0.6	Well developed	Missing	0.9-1.1 × 0.5-0.7	Globose-ovoid	Carmine, slightly bitter taste
<i>europaea</i>	3-7	White	0.4-0.5	Well developed	Missing	1-3.5 × 0.6-2	Ellipsoid to subglobose	Purplish, bitter taste
<i>guanchica</i>	3-6	White	0.4-0.5	Not well individualized or missing	Well developed	0.8-2.2 × 0.9-1.2	Ovoid-globose	Purplish, rather bitter taste
<i>cerasiiformis</i>	2-5	White	0.4	Generally present and well developed	Well developed	1.2-2.2 × 0.9-1.2	Ellipsoid	Purplish, rather bitter taste
<i>laperrinei</i>	2-3.5	White	0.4-0.6	Present and well developed	Well developed	0.5-0.8 × 0.4-0.5	Ovoid-globose	Purplish
<i>cuspidata</i>	2.5-6	White, whitish or cream	0.3-0.4	Well developed	Well developed	0.5-0.7 × 0.4-0.6	Globose or subglobose	Purple, sweet taste

Table 4. List of the plant material characterized using RAPDs, cpDNA PCR polymorphism, and mtDNA RFLPs

Subspecies/species	Locality	Latitude	Longitude	N ^a	Chlorotype ^c	Mitotype ^c
<i>europaea</i>						
Cultivar	Ten ^b	—	—	10	CE1, CE2, COM1, CCK	ME1, ME2, MOM, MCK
Oleaster	Tamanar, Morocco	32°00'N	9°33'W	10	COM1	MOM
Oleaster	Harem, Syria	36°12'N	36°31'E	13	CE1	ME1
<i>laperrinei</i>	Hoggar, Algeria	22°56'N	5°30'E	2	CE1	ME1
<i>gaunchica</i>	La Palma, Canary Islands	28°40'N	17°52'W	10	CCE1, CCE2, CCE3	MCE
<i>cuspidata</i>						
<i>O. africana</i>	Mt Elgon and Mt Kenya, Kenya	1°08'N/0°05'N	34°33'E/37°14'N	9	CA1, CA2, CA3	MAK
<i>O. chrysophylla</i>	Almihwit, Yemen	13°38'N	44°04'E	9	CC2	MIR
<i>O. cuspidata</i>	Kerman, Iran	29°00'N	57°30'E	5	CC1	MIR
<i>maroccana</i>	Immouzer-des-Ida-ou-Tanane, Morocco	30°40'N	9°10'W	5	CCE2, CCE3	MMA
	Mentaga, Morocco	30°35'N	8°50'W	3	CCE2, CCE3	MMA

^a N: number of individuals studied per population.

^b The ten cultivars were chosen from different geographical locations: 'Zaity' from Syria, 'Souri' from Lebanon, 'Gaidourolia' from Greece, 'Frantoio' from Italy, 'Giarraffa' from Sicily (Italy), 'Olivière' from France, 'Sabina' from Corsica (France), 'Picholine Marocaine' from Morocco, 'Chemlal' from Algeria, and 'Lechin de Sevilla' from Spain.

^c Data from Besnard *et al.* (2001) and Besnard *et al.* (unpubl.).

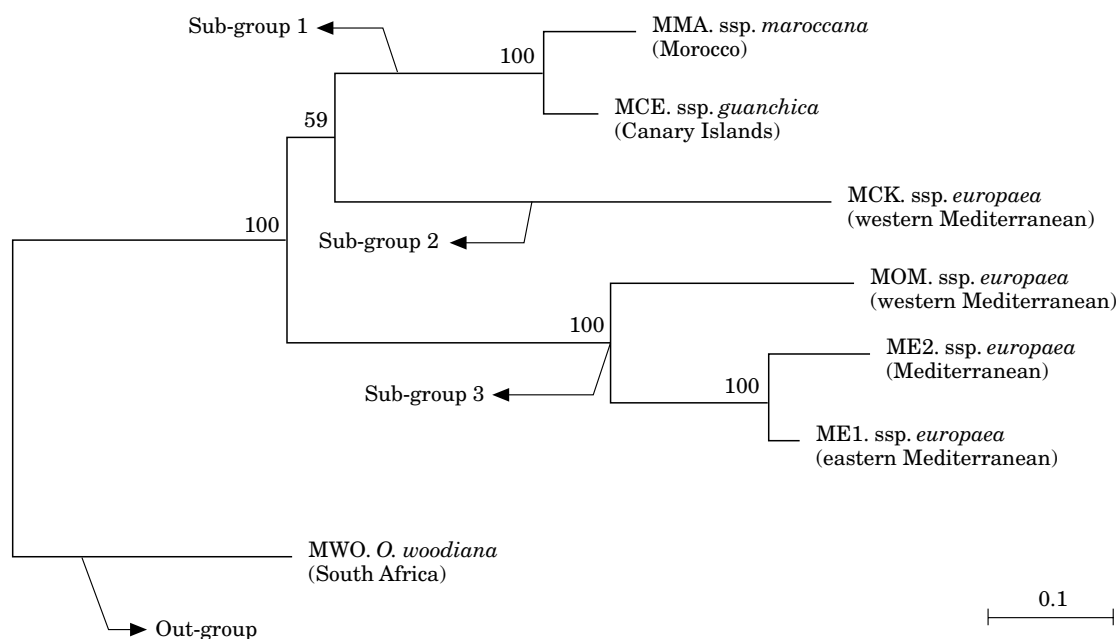


Figure 2. Phenetic tree showing the relationships between the mitotypes of North African and Mediterranean olives and constructed using Nei & Li (1979) distances and the Neighbor Joining algorithm (Nei, 1987). This analysis was based on 43 RFLPs. Bootstrap values are indicated on each node. *O. woodiana* Knobl. (from S. Africa) belonging to section *Ligustroides* Benth. & Hook., was used as an out-group to root the tree.

These molecular analyses have shown that ssp. *maroccana* displayed several specific markers (cytotypes: MMA-CCE2 and MMA-CCE3; RAPD: C15-1350, A1-250 and O8-500), and consequently, must be distinguished from the other taxa (Table 4). The genetic relationships between the mitotypes showed the existence of three groups:

- (1) One group of three mitotypes corresponding to ssp. *laperrinei* and most Mediterranean olives (ssp. *europaea*).
- (2) One mitotype (MCK) specific to the western Mediterranean (ssp. *europaea*) and associated with cytoplasmic male sterility (Besnard *et al.*, 2000).
- (3) One group corresponding to ssp. *guanchica* and *maroccana*.

The main difference with the cpDNA phylogram structure concerns the position of the Mediterranean cytotype MCK-CCK, which has been found to be related to the cytotype ME1-CE1 based on cpDNA information (Besnard *et al.*, in prep.).

Based on both cytoplasmic DNAs, ssp. *maroccana* and *guanchica* are closely related and are distinguished from the other taxa present in Mediterranean and Saharan regions. Nuclear data did not

support these relationships (Fig. 3; Hess *et al.*, 2000; Besnard, Green & Bervillé, 2001). Furthermore, despite cytoplasmic differentiation, the Oleaster population from Tamanar, located about 40 km from Imouzzèr-des-Ida-ou-Tanane (Fig. 4), is genetically close to ssp. *maroccana* as shown by RAPD analysis (on dimensions 1, 2 and 4 of the Correspondence Analysis; Fig. 3). This suggests that genetic exchanges could have occurred between these two taxa.

DISTRIBUTION

O. europaea ssp. *maroccana* has only been found within a limited area, mainly on the southern slope of the Ida-ou-Tanane massif (Fig. 4). This region is situated north and north-east of Agadir where several populations can be observed in the regions of Issi, Imouzzèr-des-Ida-ou-Tanane, Assafid, Tassademt and Ame-skroud. This taxon is also present in the region of Mentaga (north of Taroudant). Although the limits of the distribution have not been fully established, ssp. *maroccana* occupies a total area of about a few hundred hectares. Its presence in several relicual stations on the western slopes of the Souss valley and particularly in the western Anti Atlas is possible. This is attested

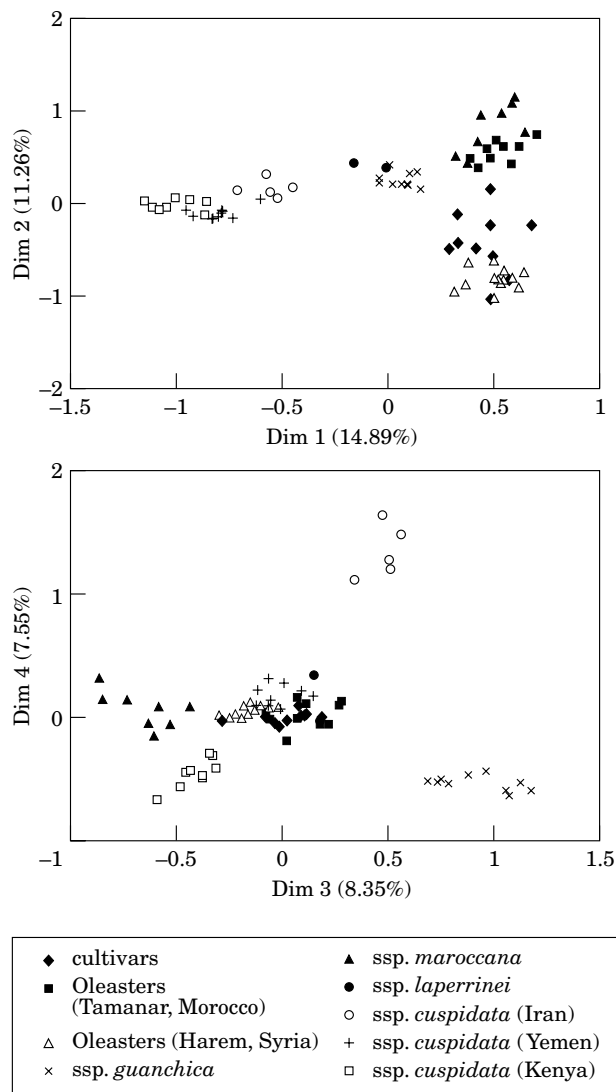


Figure 3. Correspondence Analysis (CA) based on 79 RAPD markers showing the relationships between 76 individuals belonging to different populations of the *Olea europaea* complex. The fourth first axes of the analysis were considered. The RAPD data have been previously described in Besnard *et al.* (2001).

by the recent discovery of isolated *maroccana* trees in a rupicolous situation, in the gorges of Assif Oumarhouz, 30 km north-west of Tafraoute (Fig. 4), in a locality where *Dracaena draco* L. ssp. *ajgal* Benabid & Cuzin has been discovered (Benabid & Cuzin, 1997).

HABITAT AND ECOLOGY

STRUCTURE OF THE *OLEA EUROPAEA* SSP. MAROCCANA COMMUNITY

O. europaea ssp. *maroccana* seems to be almost exclusively restricted to the plant community containing

this olive tree and *Argania spinosa* (the association of *Oleo maroccanae-Arganietum spinosae* Barbero, Benabid, Quézel, Rivas-Martinez & Santos 1982); this is an endemic phytocenosis, mainly present on the southern slopes of the Ida-ou-Tanane massif (Fig. 4). This community was initially defined using 10 phytocological relevés (Table 5) performed by Barbero *et al.* (1982) following the method of Braun-Blanquet (1964). Ssp. *maroccana* appears to be an exclusive characteristic of this biocenose, whereas the ecological optimum of *Tetraclinis articulata* (Vahl) Masters is found in this ecosystem for south-west Morocco. From a phytosociological point of view, this community can be integrated in the alliance of *Acacion gummiferae* Barbero, Quézel & Rivas-Martinez 1981, and in the order of *Acacio gummiferae-Arganetalia spinosae* Barbero, Quézel & Rivas-Martinez 1981, endemic to SW Morocco, and finally in the Mediterranean class of the *Quercetea ilicis* Braun-Blanquet 1947.

This is a moderately dense forest, which can reach 5–6 m high, mainly developed on quite deep soils. Globally, the relevés are homogeneous in terms of total plant cover, which is fairly high (80–90%), and in moderateness of slope (20–35°). Nevertheless, two clear groups can be distinguished. The first (relevés 1–6) is characterized by *Euphorbia beaumierana* Maire, *Chamaecytisus mollis* (Cav.) Greuter & Burdet, *Bupleurum dumosum* Cosson & Balansa, *Coronilla ramosissima* (Ball) Ball and *Genista ifniensis* A. Caballero. These species mainly grow in the lower levels of the Ida-ou-Tanane and they define the infra-Mediterranean level (Barbero *et al.*, 1982). The *Euphorbia beaumierana* variant harbours the greatest plant richness (16–20 species/100 m²). The second (relevés 7–10) is mainly defined by a high cover of *Argania spinosa* and the presence of *Acacia gummifera* Willd., whereas other infra-Mediterranean plants are more scarce. Compared to the *E. beaumierana* variant, this occidental variant appears to be notably species-poor (10–13 species/100 m²).

On the whole, the *Oleo maroccanae-Arganietum spinosae* community grows at between 500–800 m and 1100–1300 m altitude. At lower altitudes, the oceanic *Euphorbia officinari-Arganietum spinosae* Barbero *et al.*, 1982 community possesses a few characteristic plants (*Senecio anteuphorbium* L., *Warionia saharae* Bentham & Cosson, *Caralluma hesperidum* Maire) of the argan preforests, which seem to be absent in the Moroccan olive community. At higher altitudes, sclerophyllous holm-oak forest with *Quercus ilex* L. ssp. *rotundifolia* (Lam.) T. Morais (*Smilaci mauritanicae-Quercetum rotundifoliae* Barbero, Quézel & Rivas-Martinez, 1981) is present. In this more or less degraded community, plant species linked with the argan ecosystem are almost absent.

In its unique locality within the western Anti Atlas

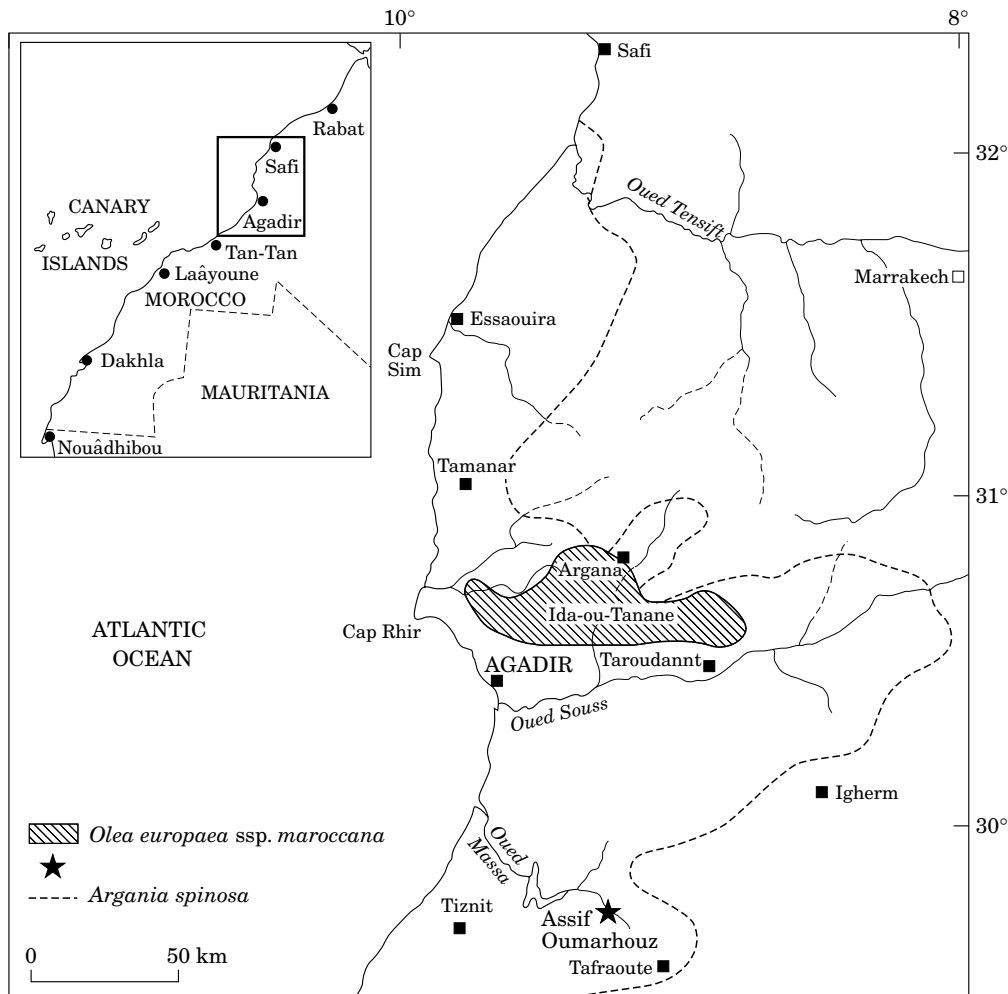


Figure 4. Distribution of *Olea europaea* ssp. *maroccana*.

(Assif Oumarhouz gorges), ssp. *maroccana* is a very rare species with a reduced cover within the endemic and species-rich rupicolous community [*Davallio canariensis*-*Dracaenetum ajgal* (Benabid & Cuzin, 1997) Médail & Quézel, 1999] where several relictual plants of south-west Morocco are present, notably the Moroccan dragon tree (Benabid & Cuzin, 1997; see Médail & Quézel, 1999: table A1, relevés 3, 6 and 7 for details of the plant assemblage). The similarity of species composition between the two areas (Ida-ou-Tanane vs. Anti Atlas) is quite low, with only 20.2% of plants in common (mainly species of the argan and holm-oak forests).

ECOLOGICAL REQUIREMENTS OF *OLEA EUROPAEA* SSP. *MAROCCANA*

O. europaea ssp. *maroccana* colonizes an altitudinal fringe between 500 and 1000 m, with some individuals present beyond these altitudes (at 440 and 1100 m) (Barbero *et al.*, 1982). For the most part, it occupies

southern slopes with gentle gradients, such as ravines, which are well exposed to oceanic influences. It seems indifferent to substrate, since it has been observed growing on limestone (particularly in the Ida-ou-Tanane massif) on sandstone and on metamorphic rocks.

There are no meteorological stations within this area, and thus the climatic data can only be approximated on the basis of those collected by Donadieu (1977) from neighbouring stations (Table 6). According to these, the ssp. *maroccana* populations fall within a low-arid or superior semi-arid bioclimate sensu Emberger, mainly at the margin between the thermo-Mediterranean and infra-Mediterranean belts (*étages de végétation*, i.e. zones of vegetation described on the basis of topography, altitude, regional climates and plant assemblages), with a mean of the maxima of the warmest month of the year (M) lying between 28 and 30°C.

The main ecological requirements of the other olive taxa of the *O. europaea* complex are summarized in Table 7. Those of ssp. *europaea* are similar to those of

Table 5. Phytocological relevés of several populations of *Olea europaea* ssp. *maroccana* (after Barbero et al., 1982, modified). Location of the relevés: 1, near Tassademt; 2, 7 km S. of Tassademt; 3, Tassademt; 4, 5 km north of Ameskrout; 5 and 6, 4 km south-west of Ameskrout; 7 and 8, Ida-ou-Tanane, near Tamharght; 9, Ida-ou-Tanane, near Zagulat; 10, pass of Zaouiel. Numerals and plus symbols indicate the classical phytosociological scale of cover and dominance. + = rare species with a low % of cover. Species with a cover of (1) <5%, (2) 5–25%, (3) 25–50%, (4) 50–75%, (5) >75%. The first numeral corresponds to the cover and the second to the ‘abundance-dominance’ of each plant. Dashes indicate that the species is absent from the releve.

	1	2	3	4	5	6	7	8	9	10
Relevés	1100	950	1000	950	680	650	500	550	650	440
Altitude	100	100	100	100	100	100	100	100	100	100
Area (m ²)	90	80	90	80	90	90	90	90	90	90
Cover	E	S	SE	E	S	S	S	SE	S	S
Aspect	30	20	20	30	30	30	25	35	30	25
Slope (°)	19	17	16	20	20	16	10	13	12	11
Specific richness										
Characteristic species of the community:										
<i>(Oleo maroccanae-Arganietum spinosae</i> Barbero et al., 1982)										
<i>Olea europaea</i> L. ssp. <i>maroccana</i> (Greuter & Burdet) P. Vargas et al.	2.3	1.3	3.4	3.4	3.3	3.3	+2	2.2	1.2	3.3
<i>Tetraclinis articulata</i> (Vahl) Masters	+	3.3	1.1	2.3	2.3	3.3	—	—	3.4	2.2
Characteristic species of the Argan preforest:										
<i>(Acacio gummiferae-Arganetalia spinosae</i> Barbero et al., 1982)										
<i>Argania spinosa</i> (L.) Skeels	3.4	1.2	2.3	1.3	2.3	1.3	4.4	3.3	3.3	3.3
<i>Lavandula dentata</i> L. var. <i>candicans</i> Batt.	2.3	—	—	3.3	—	+	1.1	2.2	+	1.2
<i>Rhus pentaphylla</i> (Jacq.) Desf.	—	1.2	—	—	1.2	1.2	+2	+2	+2	—
<i>Genista triacspidata</i> Desf. ssp. <i>sparciflora</i> (Ball) Maire	1.2	1.2	2.3	—	2.3	1.2	1.2	1.2	—	—
<i>Periploca laevigata</i> Aiton ssp. <i>angustifolia</i> (Labill.) Markgraf	2.2	1.2	1.3	2.3	3.3	—	2.2	2.3	1.2	2.3
<i>Acacia gummifera</i> Willd.	—	—	—	+	—	—	1.2	+	—	1.2
<i>Chamaecytisus mollis</i> (Cav.) Greuter & Burdet	1.2	1.2	1.3	—	—	—	—	—	—	—
<i>Bupleurum dumosum</i> Cosson & Balansa	—	—	1.2	—	1.2	—	—	—	—	—
<i>Asparagus pastorianus</i> Webb & Berth.	—	—	—	+	—	+	—	—	—	—
<i>Coronilla ramosissima</i> (Ball) Ball	—	1.2	—	—	1.2	1.2	—	—	—	—
<i>Rhus tripartita</i> (Ucria) Grande	—	—	—	—	+	—	—	—	—	—
<i>Linaria sagittata</i> (Poiret) Steudel	×	—	—	1.3	—	1.3	—	—	—	—
<i>Euphorbia beauvierana</i> Maire	3.2	+	3.3	2.3	—	—	—	—	—	—
<i>Genista ifniensis</i> A. Caballero	+	—	—	—	1.3	2.3	—	—	—	—
<i>Striga gesnerioides</i> (Bent.) Vatke	+	—	—	1.3	—	2.3	—	—	—	—
<i>Ononis natrix</i> L. subsp. <i>arganietorum</i> (Maire) Sirj.	1.1	—	+	—	—	—	—	—	—	—

continued

Table 5 – continued

	1	2	3	4	5	6	7	8	9	10
Relevés	1100	950	1000	950	680	650	500	550	650	440
Altitude	100	100	100	100	100	100	100	100	100	100
Area (m ²)	90	80	90	80	90	90	90	90	90	90
Cover	E	S	SE	E	S	S	S	SE	S	S
Aspect	30	20	20	30	30	30	25	35	30	25
Slope (°)	19	17	16	20	20	16	10	13	12	11
Specific richness										
Characteristic species of the Holm-oak forest:										
<i>(Quercetea ilicis</i> Br.-Bl. 1947)										
<i>Olea europaea</i> L. var. <i>sylvestris</i> (Mill.) Lehr.										
<i>Pistacia lentiscus</i> L.										
<i>Rhamnus lycioides</i> L. subsp. <i>atlantica</i> (Murb.) Jahandiez & Maire										
<i>Ceratonia siliqua</i> L.										
<i>Withania frutescens</i> (L.) Pauquy										
<i>Ephedra alissima</i> Desf.										
<i>Rubia pergrina</i> L. ssp. <i>longifolia</i> (Poiret) O. Bolos										
<i>Arisarum vulgare</i> Targ-Tozz.										
<i>Chamaerops humilis</i> L.										
Other species:										
<i>Drimys maritima</i> (L.) Stearn										
<i>Thymus satureioides</i> Coss.										
<i>Launaea arborescens</i> (Batt.) Murb.										
<i>Asphodelus ramosus</i> L. subsp. <i>ramosus</i>										
<i>Globularia alypum</i> L.										
<i>Fumana laevipes</i> (L.) Spach										
<i>Lavandula maroccana</i> Murb.										
<i>Eryngium ilicifolium</i> Lam.										
<i>Phagnalon saxatile</i> (L.) subsp. <i>saxatile</i>										
<i>Piptatherum miliaceum</i> (L.) Coss.										
<i>Teucrium polium</i> L.										
<i>Salvia aegyptiaca</i> L.										
<i>Lavandula multifida</i> L.										
<i>Brachypodium distachyon</i> (L.) P. Beauv.										

Table 6. Bioclimatic data from the nearest meteorological stations for the populations of *Olea europaea* ssp. *maroccana* (following Donadieu, 1977)

Meteorological station	Altitude (m)	Annual rainfall (mm)	M ^a (°C)	m ^b (°C)	Number of dry months
Agadir	50	226	27.1	7.2	9
Taroudannt	255	231	36.3	5.1	—
Tamanar	360	313	37.4	6.8	7
Argana	750	176	41.2	2.2	9
Immouzzzer-des-Ida-ou-Tanane	1310	493	33.8	4.8	5

^a M: mean of the maxima of the warmest month of the year.

^b m: mean of the minima of the coldest month of the year.

Table 7. Main ecological requirements of *Olea europaea* ssp. *maroccana*, compared to the other taxa of the *O. europaea* complex

Subspecies of the <i>Olea europaea</i> complex	Chorology	Altitude (m)	Substrate	Pann. (mm)
<i>maroccana</i>	SW Morocco	(440)500–1000(1100)	Various	300–450
<i>europaea</i>	Mediterranean Basin	0–800(1700)	Various	(200)400–800(1000)
<i>guanchica</i>	Canary islands	0–600(1000)	Volcanic rocks	200–600
<i>cerasiformis</i>	Madeira islands	0–500	Volcanic rocks	340–650
<i>laperrinei</i>	Sahara	1500–2700	Eruptive rocks Volcanic rocks	50–90
<i>laperrinei</i>	Sahel	1800–2800	Volcanic rocks	150–900
<i>cuspidata</i>	Mediterranean S. Africa (i.e. Cape Region) Tropical and arid Africa	0–800 800–2800	Various Various	400–800 200–800

Subspecies of the <i>Olea europaea</i> complex	m (°C)	Bioclimate	Length and main season of the dryness	Vegetation belts
<i>maroccana</i>	3.5–6	Arid, semi-arid	6–8 months; summer	Infra-Mediterranean Thermo-mediterranean
<i>europaea</i>	3–12	(Arid), semi-arid, sub-humid (humid)	3–7 months; summer	(Infra-Mediterranean) Thermo-Mediterranean Meso-Mediterranean
<i>guanchica</i>	3.5–14	Arid, semi-arid	3–10 months; summer	Infra-Canarian, Meso-Canarian
<i>cerasiformis</i>		Arid, semi-arid		Thermo-Canarian
<i>laperrinei</i>	0.3	Saharian	± 12 months; variable	Montane-Saharan
<i>laperrinei</i>	7–14	Sahelian arid, semi-arid	5–8 months; winter	Montane-tropical
<i>cuspidata</i>	6–4 6–14	Semi-arid, sub-humid Arid, semi-arid, sub-humid	3–7 months; summer 3–9 months; winter	Thermo-Mediterranean Montane-tropical

ssp. *maroccana*, notably for temperature, rainfall, and extent of dry season (3–7 months on average). The Macaronesian olives (ssp. *cerasiformis* and *guanchica*) are also found in similar ecological situations,

although their extension into the infra-Canarian belt is more accentuated than that of ssp. *maroccana* at the infra-Mediterranean level. Indeed, the Macaronesian olives can be found on the coastline, which is never

the case for ssp. *maroccana*, and they are not found beyond 900–1000 m, i.e. they do not reach the meso-Canarian belt (Rivas-Martinez *et al.*, 1993). They can withstand a marked period of summer drought (3–10 months), if we do not consider dew and fog rainfalls. *O. europaea* ssp. *laperrinei* is characterized by two major types of population (Fig. 1), heterogeneous in their ecology. In the high central Saharan mountains of the Hoggar and neighbouring massifs (Maire, 1933; Benichou, 1962; Quézel, 1965) and in the Northern Aïr (Gréboun region: Quézel, 1962), it grows in a Saharan bioclimate, between 1600 and 2700 m. In this situation, water requirements are very much less than of ssp. *maroccana*, since the dry season continues throughout the year. The other populations, distributed in the Sahelian Afro-tropical region (Central-Southern Aïr: Bruneau de Miré & Gillet, 1956; Poilecot, 1996; Jebel Marra: Wickens, 1976; Miehé, 1988; Gourgueil: Quézel, 1969), are subject to different ecological conditions, since rainfall is associated with the monsoon (mainly between August and October), and consequently follows a tropical rhythm. *O. europaea* ssp. *cuspidata* occupies a large area in Africa, from the Cape to the mountains surrounding the Red Sea. This taxon displays a variety of ecological requirements which reflect its taxonomic complexity. Its northernmost populations, located near the Red Sea (Fig. 1), on the Jebel Elba and the Jebel Qattar, grow in a semi-arid and a subdesert bioclimate, respectively (Boulos & Hobbs, 1986).

DISCUSSION

TAXONOMIC POSITION OF THE MOROCCAN OLIVE

According to our results, the Moroccan olive must be differentiated from the other taxa of the *O. europaea* complex because it presents distinctive morphological, molecular and ecological characters. Its taxonomic position has long remained uncertain because it shares morphological traits with the other subspecies (*europaea*, *laperrinei*, *cerasiformis*, *guanchica*) of North Africa and Macaronesia. However, these shared characters may differ. Differences in leaf morphology (width and length/width) between ssp. *maroccana* and *europaea* are useful for distinguishing these two sympatric taxa. The existence of well developed bracteoles on the floral pedicel for ssp. *maroccana*, *cerasiformis* and *cuspidata*, but not for *europaea* and *guanchica* is a relevant observation and suggests the existence of two lineages.

Nuclear and cytoplasmic DNA polymorphism reveal that ssp. *maroccana* is a well-differentiated taxon. Our molecular results are in agreement with those of Hess *et al.* (2000), even though these authors do not taxonomically distinguish ssp. *maroccana*. Nevertheless,

it is very close to ssp. *guanchica* on the basis of cytoplasmic DNA polymorphism (Fig. 2), and to oleasters from the western Mediterranean Basin on the basis of nuclear DNA data (Fig. 3). In contrast, ssp. *laperrinei* is genetically distinct from ssp. *maroccana*, refuting the opinions of Sauvage & Vindt (1952) who considered the latter to be an intermediate form between ssp. *europaea* and *laperrinei*, and of Green & Wickens (1989) and Zohary & Hopf (1994), who included it in ssp. *laperrinei*. Thus, the putative affinities between the Moroccan and the Saharan olive, based mainly upon often subjective morphological criteria and a single ISSR analysis (Hess *et al.*, 2000) are in fact quite weak.

Nevertheless, there are discrepancies between the morphological and molecular data, which can be explained by two hypothetical factors:

- (1) The occurrence of common characters could result from independent convergent evolution of some characters in genetically well-differentiated taxa (for instance, the lanceolate leaf is an adaptation to drought).
- (2) The taxa from North Africa share a common genetic background, explaining the persistence of common ancestral characters. Moreover, gene exchanges between these taxa could also have occurred after their differentiation.

Evaluation of the biogeographical and ecological data may enable us to consider these hypotheses. With regards to the morphological and molecular results, we consider that the Moroccan olive is more accurately ranked as a subspecies of *Olea europaea*, in agreement with the recent proposal of Vargas *et al.* (2001). This choice must be defended because previous authors (Barbero *et al.*, 1982; Greuter & Burdet, 1989) have considered it to be a species. Their arguments are sustained by the existence of morphological differences, notably the presence of terminal inflorescences, and the criterion of reproductive isolation *sensu* Mayr (1942). Nevertheless, the relative morphological and genetic closeness to ssp. *guanchica* and *europaea*, and the not yet strictly demonstrated sexual isolation encourage us to cautiously retain the sub-specific level. This placement is also in agreement with that of Green & Wickens (1989) for the other taxa of the *O. europaea* complex.

BIOGEOGRAPHY AND PROBABLE ORIGIN OF *OLEA EUROPAEA* SSP. *MAROCCANA*

In Central and Mediterranean Europe, the first fossil remains of the genus *Olea* appeared during the Tertiary era, as since the Oligocene, several taxa of the ancestral group *Olea notii* (*O. notii* Ung., *O. oleastroides* Zabl., *O. moldavica* Negru) close to *O. europaea*, are mentioned

(Palamarev, 1989). In the western part of the Mediterranean Basin, fossilized *Olea* pollen, still rare during the early Miocene (Suc, 1989), has become more frequent during the early Pliocene (Zanclean: 5.3–4.5 Mya). Thus, olive trees were probably a major component of sclerophyllous matorrals (maquis), quite similar to the actual plant communities present at the thermo-Mediterranean level (Suc *et al.*, 1995). The Mediterranean olive persisted in several ice age refugia during the Palaeolithic since *Olea* pollen is found quite regularly in prehistoric sites dating back at least 800 000 years (Couplan, 1996).

In North Africa, the drastic climatic events occurring with some periodicity since the end of the Miocene (including the progressive desiccation of the Maghreb with extension of Sahelian-type vegetation, and the desertification of the Sahara linked to lower temperatures) have had a major impact on the structure of plant communities (cf. Quézel & Barbero, 1993). It would appear that populations of Mediterranean olive trees were probably pushed back into more favourable areas, along the Atlantic coast of North Africa and on the recently emerged Macaronesian Islands. After the Pleistocene, olive trees appear again as a significant element of the thermo-Mediterranean maquis in the Iberian Peninsula (Badal *et al.*, 1994; Yll *et al.*, 1996) and in Mediterranean France (Solari & Vernet, 1992). In the High Atlas range, major finds of *Olea* pollen have been dated to the Boreal (Bernard & Reille, 1987) (a very dry period, between 8000–9000 BP). However, it is impossible to allocate them with any confidence to the different taxa of the *O. europaea* complex (Nilsson, 1988; Reille, pers. comm.). We must emphasize that ssp. *maroccana* is probably not implicated in the domestication process of the cultivated olive of North Africa, since the latter was much more recently cultivated (around 1000 BP) in the High Atlas (Bernard & Reille, 1987).

The molecular findings (Besnard & Bervillé, 2000) have supported the *O. europaea* complex as a characteristic example of a tropical African lineage, of which three different evolutionary units have later colonized several distinct areas, notably North Africa and the Mediterranean Basin. According to cpDNA and mtDNA analysis, ssp. *guanchica* and *maroccana* are very closely related, suggesting their quite recent divergence from a common ancestor. These data support the conclusion that they belong to the same sub-phylum and are distinct from the other Mediterranean and Saharan forms. Furthermore, a relatively high cytoplasmic diversity has been maintained in these populations (Table 2). All of which suggests that ssp. *maroccana* is a relictual taxon, since populations newly colonizing an area should display a low cytoplasmic diversity (Petit *et al.*, 1993). Nevertheless, high cytoplasmic diversity in a population could also be due to

successive waves of migration. This is frequently found in the olive (Besnard & Bervillé, 2000), although in those cases, several non-related lineages are mixed.

The foregoing paleogeographic, morphological and molecular data, and also the restricted distribution, support ssp. *maroccana* as a relictual tree, probably differentiated from an ancestral unit of tropical Africa. Several phytogeographers (e.g. Chevalier, 1948; Quézel, 1965, 2000; Maley, 1980) have argued that important floristic exchanges occurred between tropical Africa and the Mediterranean Basin. The migration of the ancestral *Olea* probably occurred prior to the desertification of the Sahara and dates at least from the Pliocene. The Moroccan and Macaronesian olives could be derived from this ancestor, which had colonized North Africa before its collision with the Eurasian plate. As stated by Hewitt (1996, 1999), the emergence of mountain ranges generally produces considerable genomic reorganization and speciation events, particularly important around the refugia. Thus, divergence of the Moroccan and Macaronesian olives may have been possible due to severe Plio-Pleistocene climatic events (Quézel & Barbero, 1993). In the Macaronesian Islands and south-west Morocco, olive trees were subjected to different ecological pressures and some morphological and genetic differences have appeared (Hess *et al.*, 2000; Besnard *et al.*, in prep.). Nevertheless, the strong affinities based on ctDNA between these taxa suggest a quite recent differentiation. The colonization of the Canary archipelago by the olive is consistent with a stepping-stone model of directional east–west migration (Hess *et al.*, 2000). Furthermore, combined molecular studies (ISSR-PCR and RAPD) have revealed that the olives from the Canary Islands and Madeira form two separate clusters and taxa, suggesting at least two independent dispersal events from the African coast, the first one being towards Madeira (Hess *et al.*, 2000). As in others fleshy-fruited trees (*Laurus azorica* (Seub.) Franco, *Dracaena draco*), the inter- and intra-archipelago colonizations can be explained by long-distance ornithochoric dispersal.

This biogeographical scheme is consistent with the occurrence of several tropical plant species in Morocco (*Argania spinosa*, *Acacia gumifera*, *Commelina rupicola* Font-Quer, *Kalanchoe laciniata* (L.) DC. ssp. *faustii* (Font-Quer) Maire, *Warionia saharae*), in the Canary Islands (*Canarina*, *Sideroxylon*, *Ceropegia*), or both areas (*Dracaena draco*, *Sonchus* sect. *Dendrosonchus*, *Aeonium*, *Caralluma*, *Euphorbia*) (Bramwell, 1985; Quézel, 1995; Médail & Quézel, 1999). The biogeographical relationships between south-west Morocco and the Canary Islands are also strongly supported by recent phylogenetic studies of several animal groups (Juan *et al.*, 2000). Because of

the oceanic influences inducing important fog precipitations and the highly contrasted Atlas relief, several parts of south-west Morocco act as refugia, and the rate of vascular plant endemism is *c.* 9% (Médail & Quézel, 1999). Thus, the relictual position of ssp. *maroccana* seems to be well established, and this fact implies that specific conservation measures have to be taken.

THREATS AFFECTING THE POPULATIONS OF *OLEA EUROPAEA* SSP. *MAROCCANA* AND CONSERVATION STATUS

O. europaea ssp. *maroccana* populations are threatened by several factors and a conservation programme should be implemented in the near future in order to ensure their survival.

The first threat is related to the limited distribution area and reduced size of populations. These are very fragmented and probably correspond to a critical size for the long-term viability of the species.

The second threat is presented by human and livestock pressure, which damages most North African ecosystems (e.g. Barbero *et al.*, 1990; Quézel, 1991). Because of the demographic increase in the Maghreb, plant populations in Morocco are seriously affected by humans, even though agricultural systems with *Argania spinosa* have remained largely traditional. It is not surprising that not a single individual of considerable age or height has been found. In fact, intensive cutting back, which is regularly performed about every 20 years by local communities for firewood or charcoal, is a traditional and ancient practice. With the exception of *Argania spinosa* which is preserved as a fruit species, the other phanerophytes, and particularly *Tetraclinis articulata*, are threatened in much the same way. Overgrazing is another serious problem in Morocco, because it can seriously limit plant regeneration by affecting the seedling recruitment of *Olea*, which is already low due to the dry conditions (Rey & Alcántara, 2000). This phenomenon occurs in Ida-ou-Tanane, as indicated by the high frequency of unpalatable geophytes such as *Asphodelus ramosus* L. ssp. *ramosus* and *Drimia maritima* (L.) Stearn (see Table 5).

The third threat relates to gene flow between individuals of this taxon and ssp. *europaea* (oleasters, feral and cultivated forms) with a sympatric distribution. Gene exchange between wild and cultivated forms of ssp. *europaea* has been demonstrated by Besnard & Bervillé (2000), and a phylogeographic study of the *O. europaea* complex supports the occurrence of several gene exchange events between different taxa throughout the evolution of the olive (Besnard, Green & Bervillé, 2001). Furthermore, the relative genetic

proximity displayed by RAPD markers of sspp. *maroccana* and *europaea* could be explained by some introgressions. In this case, gene exchange should be assessed and quantified in order to preserve ssp. *maroccana* populations which are the least introgressed. Nevertheless, gene exchange seems to be very limited because the flowering period of ssp. *maroccana* occurs 30 to 40 days after that of ssp. *europaea* (Besnard & Khadari, pers. obs.); Hess *et al.* (2000) have also suggested that little or no gene flow occurs between the cultivated and native olives in the Macaronesia islands.

Of all these threats, the most important is that posed by human pressure; the other two probably have a limited effect due to the long-term viability of the taxon. In fact, the effect of the reduction in size of ssp. *maroccana* populations can be compensated for by several biological features (long living woody species, possible regeneration from stubs, adaptation to different ecological conditions). Because of human pressure, the Moroccan olive is one of the ten most threatened trees in the Mediterranean Basin (Barbero *et al.*, 2001). Today, this endemic taxon is not listed in the most recently published international *Red Books* (Walter & Gillett, 1998; Oldfield, Lusty & McKinven, 1998). It should be listed as vulnerable (VU) according to the new classification of the IUCN (1994).

In situ conservation of ssp. *maroccana* populations is a priority for its long-term viability. It is important to assess critical population size and determine the crucial stages involved in the recruitment dynamics of this tree, in comparison with the wild olive (Rey & Alcántara, 2000). Future studies should also focus on genetic structure and reproductive biology (duration and time of flowering) of the Moroccan olive populations, and take into account different ecological conditions, which have a notable impact on population structure (altitudinal and latitudinal gradients, presence of western variant of *Acacia gumifera* and eastern variant of *Euphorbia beaumierana*). Some populations are located within the new Moroccan system of preserved areas (SIBE: *Site d'Intérêt Biologique et Ecologique*). However, the success of any conservation programme depends on continuous dialogue with, and the involvement of, local communities (Alifriqui, Benchaâbane & Jaafar, 1995).

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APPENDIX

PLANT MATERIAL: HERBARIUM SPECIMENS EXAMINED

Olea europaea L. ssp. *maroccana* (Greuter & Burdet)
P. Vargas, J. Hess, Muñoz Garm. & Kadereit

S.W. Morocco, Ida-ou-Tanane, near Tamrhakht, P. Quézel, iv.1982 (MARSSJ TYPUS) (inflorescence); Ida-ou-Tanane, P. Quézel, 01.iii.1990 (MARSSJ) (infructescence); Imouzzet-des-Ida-ou-Tanane, P. Quézel,

xi.1993 (MARSSJ) (infructescence); Imouzzer-des-Ida-ou-Tanane, P. Quézel, xi.1993 (MARSSJ) (2 sheets, sterile ramet); Ameskrout, leg. S. Muller, F. Médail, iv.2000 (MARSSJ) (3 sheets, sterile ramet); oued Tamrhakht, leg. S. Muller, F. Médail, iv.2000 (MARSSJ) (sterile ramet); cultivated specimen at the INRA Montpellier from a south-west Moroccan individual, leg. C. Breton, F. Médail, 28.iv.2000 (MARSSJ) (inflorescence); Imouzzer-des-Ida-ou-Tanane, cultivated specimen at the INRA Montpellier, leg. G. Besnard, F. Médail, x.2000 (MARSSJ) (infructescence).

Olea europaea L. ssp. *europaea*

France, Bouches-du-Rhône, Coudoux, wild individual, F. Médail, 02.ix.2000 (MARSSJ) (infructescence); Bouches-du-Rhône, Marseille, Le Merlan, 100 m, M. Gruber, 28.v.1972, n°1554 (MARSSJ) (inflorescence); Bouches-du-Rhône, Marseille, M. Gruber, 18.iv.1972, n°1298 (MARSSJ) (sterile ramet); Var, Carqueiranne, entre San Salvador et Olbia près de la mer, wild individual, F. Médail, 20.viii.2000 (MARSSJ) (sterile ramet); Var, Carqueiranne, terrasses du Bau Rouge, wild individual, F. Médail, 20.viii.2000 (MARSSJ) (infructescence); Var, Le Pradet, Cap Garonne, wild individual, F. Médail, 25.viii.2000 (MARSSJ) (sterile ramet). South-west Morocco, oued Tamrhakht, leg. S. Muller, F. Médail, iv.2000 (MARSSJ) (sterile ramet). Canary islands, Gran Canaria, monte Tafira, 350 m, leg. G. Kunkel, sub *O. europaea* ssp. *oleaster?*, 06.i.1972 (G: 115168) (sterile ramet); Gran Canaria, Atalaya, 600 m, leg. G. Kunkel, sub *O. europaea* cf. ssp. *europaea*, 11.iii.1966 (G: 115165) (inflorescence). Algeria, Kabylie, Tizi Ouzou, cultivated specimen at the INRA Montpellier, leg. G. Besnard, F. Médail, x.2000 (MARSSJ) (sterile ramet). Libya, Benghazi, cultivated specimen at the INRA Montpellier, leg. G. Besnard, F. Médail, x.2000 (MARSSJ) (sterile ramet).

Olea europaea L. ssp. *guanchica* P. Vargas, J. Hess, Muñoz Garm. & Kadereit

Canary islands, leg. M. Despréaux, sub *O. europaea* L., 1837 (G) (2 sheets, inflorescence & infructescence);

Teneriffe, in sylvis siccoribus, leg. E. Bourgeaux, sub *O. europaea* Bertol., 1845 (G) (4 sheets, inflorescence); Gran Canaria, Atalaya, 650 m, cultivado ?, col. & det. G. Kunkel, 11.iii.1966 (G: 120078) (inflorescence); Gran Canaria, Monte Lentiscal, 500 m, en matorral, col. & det. G. Kunkel, 03.ii.1966 (G: 120079) (inflorescence); Gran Canaria, Friaga de ?, 600 m, col. & det. G. Kunkel, 16.xi.1966 (G: 115158) (infructescence); Gran Canaria, Monte Tafira, 330 m, col. & det. G. Kunkel, 28.xii.1972 (G: 115159, 115160, 115161 & 115162) (4 sheets, sterile ramet); Gran Canaria, Monte Tafira, 400 m, en matorral, col. & det. G. Kunkel, 06.iv.1967 (G: 14068) (inflorescence); Gran Canaria, Monte Tafira, col. & det. G. Kunkel, 09.xii.1970 (G: 115164) (infructescence); Gran Canaria, Barranco de Guinguada, 250 m, col. & det. G. Kunkel, 27.iii.1969 (G: 115163) (inflorescence).

Olea europaea L. ssp. *cerasiformis* (Webb. & Berth.) Kunkel & Sunding

Madeira, Funchal, propre Praia formosa, leg. J. Bornmüller, 12.iv.1900 (G) (sterile ramet); Madeira, in rupestris, Poco da Neve, 500 m, leg. G. Mandon, sub *O. europaea* L., 14.v.1865 (G) (3 sheets, infructescence); Madeira, in rupestribus maritimis, Cabo Girão, leg. G. Mandon, sub *O. europaea* L., 12.vi.1868 (G) (3 sheets, inflorescence); Madeira, in rupibus insulae, Porto Santo, ad cacumen montis Pico d'Anna Ferreira, leg. G. Mandon, sub *O. europaea* L., 11.v.1866 (G) (2 sheets, sterile ramet); Madeira, above the bridge beyond Câmara de Lobos, leg. R.F. Lowe, sub *O. europaea* L. var. *maderensis* Lowe, 15.iii.1835 (G) (infructescence).

Olea europaea L. ssp. *laperrinei* (Batt. & Trab.) Cif.

Sudan, Darfur, C.N.R.S. Mission Botanique de la R.C.P. 45, P. Quézel & P. Bourreil, ix.1967 (MARSSJ) (inflorescence); Sudan, Gourgeil, C.N.R.S. Mission Botanique de la R.C.P. 45, P. Quézel & P. Bourreil, ix.1967 (MARSSJ) (2 sheets, inflorescence); La Source, cultivated specimen at the INRA Montpellier, leg. G. Besnard, F. Médail, x.2000 (MARSSJ) (sterile ramet).