

Distribution, shape and clonal growth of the rare endemic tree *Olea europaea* subsp. *laperrinei* (Oleaceae) in the Saharan mountains of Niger

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Abstract The populations of the Laperrine's olive (*Olea europaea* subsp. *laperrinei*) are located in three main areas corresponding to the mountains of northern Niger (Aïr), southern Algeria (Hoggar), and north-western Sudan (western Darfur). The populations native of Niger were found to occur in very fragmented patches from 1550 to 1850 m in five isolated mountains with population sizes not exceeding 100 trees each, except in the Tamgak. Samples in the Tamgak and the Bagzane mountains were studied by combining field observations with identification of genets (using highly variable DNA marker analyzes). Trees were relatively small and multi-stemmed like those in the Hoggar, and were associated with some tropical species as in the western Darfur. They were found on borders of "wadis", i.e., temporary water courses, in ravines and on hillsides. They were unable to rely on sexual reproduction, which was found to be ineffective. In contrast, 28% of the genetic profiles

found ($n_{\text{genet}} = 98$) were represented with two or more trees without aboveground connections. Molecular and morphological data both demonstrated that the populations used clonal growth (CG) to survive in the current unfavorable period of hyper-aridity, and thus are likely to be remnant populations. Signs of human-related disturbances, recorded on 43% of the sampled trees, should be a determining factor of distribution as well. In the Bagzane mountains especially, where human activities are more intense than in the Tamgak mountains, trees developed preferentially on hillsides and ravines with low access rather than on wadi borders with better edaphic conditions but easier access for livestock/people. CG may be therefore, a survival strategy both against aridity and human-related disturbances. Sexual reproduction may be triggered during a less arid period, following the model of multiple demographic strategies, widespread in arid environments. However, survival would be affected by browsing and cuttings. Lastly, the absence of an efficient sexual strategy coupled with the high fragmentation of very small populations and a narrow altitudinal range of distribution indicates that today the populations of *O. e. laperrinei* in the Aïr mountain range are more endangered than those from southern Algeria and north-western Sudan.

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Introduction

In the face of the sixth phase of species extinction, astonishing and for the first time generated by human beings (Vitousek et al. 1997; Chapin III et al. 2000), the urgent need for the conservation of biodiversity is global. It is particularly neglected in the developing countries of the Sahara. However, the desertification that has followed in the wake of a hyper-arid climatic phase (Le Houérou 1997) and the rapid growth of human populations, which leads to local overexploitation of the vegetation, invasion of exotic species and erosion (Anthelme et al. 2006), threaten to eradicate a large number of taxons that are resources for human populations and/or remarkable components of biodiversity through their endemism and their rarity (Child 2003; McNeely 2003). This threat applies especially to the ecosystems of the Saharan mountains of Niger, Africa, which are efficient refuges for vegetation diversity (Ozenda 2004), but are increasingly used as human-related resources for a few decades (Anthelme et al. 2006).

Among endangered taxa, *Olea europaea* L. subsp. *laperrinei* (Batt. and Trab.) Ciferri (Oleaceae) or Laperrine's olive is one of the most remarkable endemic tree taxa of the Sahara along with *Myrtus nivellei* and *Cupressus dupreziana* (Bruneau de Miré and Gillet 1956b; Quézel 1978; Abdoun and Beddief 2002). It belongs to the *O. europaea* complex and displays close affinities with the Mediterranean olive (Green 2002). However, genetic studies have recently revealed a complex biogeographic history for the Laperrine's olive populations, which may be due to recurrent migration events from both Mediterranean and Tropical Africa (Hess et al. 2000; Besnard et al. 2002, 2007). This wild olive tree also presents traits of potential interest for the cultivated olive. Particularly, it could be an important genetic resource for drought adaptation.

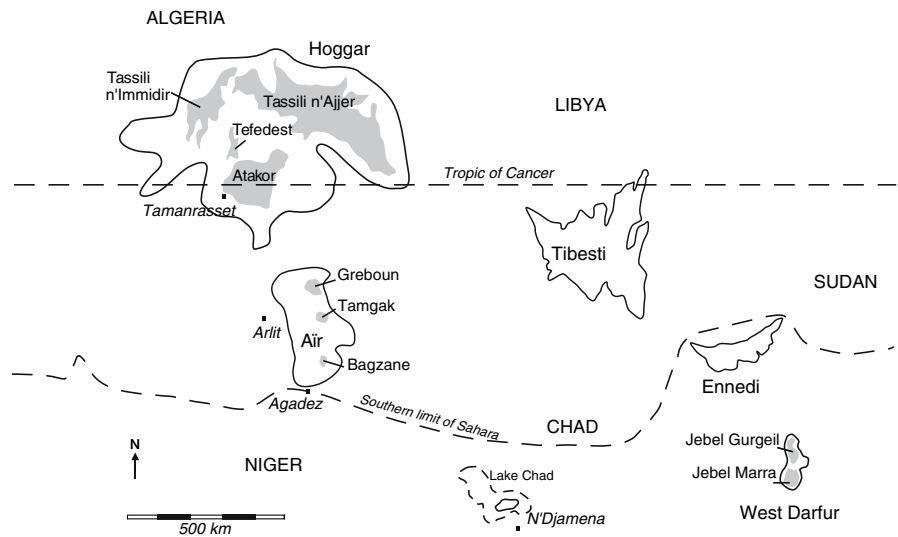
The distribution of the Laperrine's olive is limited to the Saharo-Sahelian mountain areas (Benichou 1962; Wickens 1976; Baali-Cherif and Besnard 2005; Fig. 1). In Algeria, it is found in the Hoggar mountain range, especially in the Atakor, the Tassili n'Immidir, the Tefedest, and the Tassili n'Ajjer mountains (Benichou 1962). In Niger, it has been identified in the Air mountain range in the southern Sahara and located precisely in three massifs: Greboun, Tamgak and Bagzane (Bruneau de Miré and Gillet 1956a). In

Sudan, the Laperrine's olive is present in the western Darfur (Jebel Marra and Jebel Gurgeil; Quézel 1969; Wickens 1976). Surprisingly, the Chadian mountain ranges of the Ennedi and the Tibesti do not harbour *O. e. laperrinei* today. However, fossils, indicating their existence as far back as the Pleistocene, have been discovered (Quézel 1978). Lastly, its presence in Morocco (Wickens 1976) was questioned (Maire 1933; Maley 1980) but finally refuted in favour of another endemic taxon, *O. europaea* subsp. *maroccana* (Médail et al. 2001; Vargas et al. 2001).

In all these mountain ranges, *O. e. laperrinei* is distributed only at elevations above 1200 m (Bruneau de Miré and Gillet 1956a, b; Quézel 1962, 1969; Wickens 1976; Poilecot 1996; Ozenda 2004). This characteristic makes it a Saharan mountain species *sensu* White (1983). While its numbers remain low overall, given its restricted area of distribution, *O. e. laperrinei* is frequently found in the Hoggar, the Tefedest, the Tassili n'Ajjer, (Quézel 1965), the Jebel Marra (Wickens 1976) and the Jebel Gurgeil (Quézel 1969). By comparison, the populations of the Laperrine's olive seem to be very limited in the Air mountain range (Quézel 1962; Poilecot 1996). The rarity of sexual reproduction is one of the most remarkable life-traits of *O. e. laperrinei* in the Hoggar (Quézel 1965; Baali-Cherif and Besnard 2005). This leads to think that these populations were relictual and may survive through clonal growth (CG), which can be a prevailing strategy of persistence in constrained environments (Honnay and Bossuyt 2005) under the respective influences of stress, disturbance, competition, or a combination (Anthelme et al. 2002). In contrast, sexual reproduction is efficient in Darfur where aridity is much lower (Wickens 1976; White 1983).

The populations in the Air mountain range have been poorly described, and data available are out of date and do not mention their reproduction strategies. In the Bagzane mountains, *O. e. laperrinei* was described only once (Bruneau de Miré and Gillet 1956a), and its existence is today questioned by the inhabitants themselves (Djibrilla unpublished data). However, as the populations of *O. e. laperrinei* in the Tibesti and Ennedi mountain ranges are now extinct, the populations of the Air are the last representatives of the Sahara-Sahel transition zone. Their conservation was thus made a priority during the establishment of the National Nature Reserve of the

Fig. 1 Distribution of *Olea europaea* subsp. *laperrinei* in the Saharan–Sahelian region (grey areas)



Aïr-Ténéré, but the means allocated to this task are non-existent.

Baali-Cherif and Besnard (2005) mentioned that *O. e. laperrinei* in the Hoggar (Algeria) was a small multi-stemmed tree, thus suggesting that the Laperrine's olive may use a vegetative strategy for its reproduction and persistence in arid environments. In contrast, in the wetter western Darfur, *O. e. laperrinei* was described as a tree reaching up to 15 m high without mention of a multi-stemmed shape (Quézel 1969; White 1983). Considering this variability, the description of its shape (height, maximal length at ground level if the tree is multi-stemmed) and the number of interconnected stems per tree should be relevant descriptors to understand the long-term dynamics of *O. e. laperrinei* in the Aïr. Taking into account that the Laperrine's olive has been described as strongly damaged by human-related disturbances in the Hoggar (Sahki and Sahki 2004) and in the western Darfur (Quézel 1969; Wickens 1976), signs of human-related damages should be relevant descriptors as well.

In parallel with a necessary description of the shape of *O. e. laperrinei* populations in the Aïr, the focus of the study was to determine at which level their current persistence was dependent on CG, and if they follow the model of multiple demographic strategies, alternating sexual and asexual regenerations with changes in environmental constraints (Garcia and Zamora 2003). Based on hyper-variable microsatellite loci, genetic data extracted from leaves of *O. e. laperrinei* were provided to test the existence of clonality, i.e., the occurrence of genets represented

by several trees without aboveground connections. The shape, distribution and reproductive strategies of *O. e. laperrinei* were correlated with the biotic and abiotic environments by combining field observations with genotype identification.

Material and methods

Study area

The Aïr is an ancient crystalline mountainous complex located in northern Niger between 17°N and 20°30'N and 7°30'E and 10°E, over an area of 61,500 km² (Black et al. 1967). It forms part of the southern Sahara (Ozenda 2004) as an extension of the Hoggar (southern Algeria). The elevation ranges from 700 m (rocky plateaux and plains with wadis) to 2022 m at Idoukal n'Taghès in the Bagzane mountains. The mountains are crystalline, forming plateaux surrounded by cliffs, and displaying a few volcanic intrusions (Black et al. 1967).

The principal mountains, or massifs, are the Greboun, the Tamgak, the Taghmert, the Takolkouzet, the Goundai, the Egalah-Aroyan and the Bagzane (Fig. 2). They are isolated from one another by wide plains with wadis and/or rocky plateaux. While the Greboun mountains form an integral part of the Aïr range from the geological point of view (Black et al. 1967), they are differentiated by floristic criteria that are more closely related to the southern zones of the Hoggar in Algeria (Quézel 1962).

The Bagzane mountains rise above the plains of the Air and cover an area of 40 km long and 20 km wide. The summit is a plateau (1400–1800 m) with a substratum made up of alternate layers of rock and clay-sand on granite or volcanic bedrock. Since the Neolithic age, the clay-sand zones have been a precious resource for settled populations who practice irrigated agriculture and free-range livestock farming (Adamou and Morel 2005). The Tamgak mountains cover an area substantially larger than that of the

Bagzane and their plateaux at the summit, located at the same elevation, are essentially rocky and granitic. Human populations have not taken permanent residence in these mountains that they use only occasionally for herding on an extensive basis (Giazzi 1996).

Rain falls from June to September and reaches between 20 and 100 mm year⁻¹ at elevations under 1000 m (Giazzi 1996) with a high spatial variation. They decrease however from the south-western to the

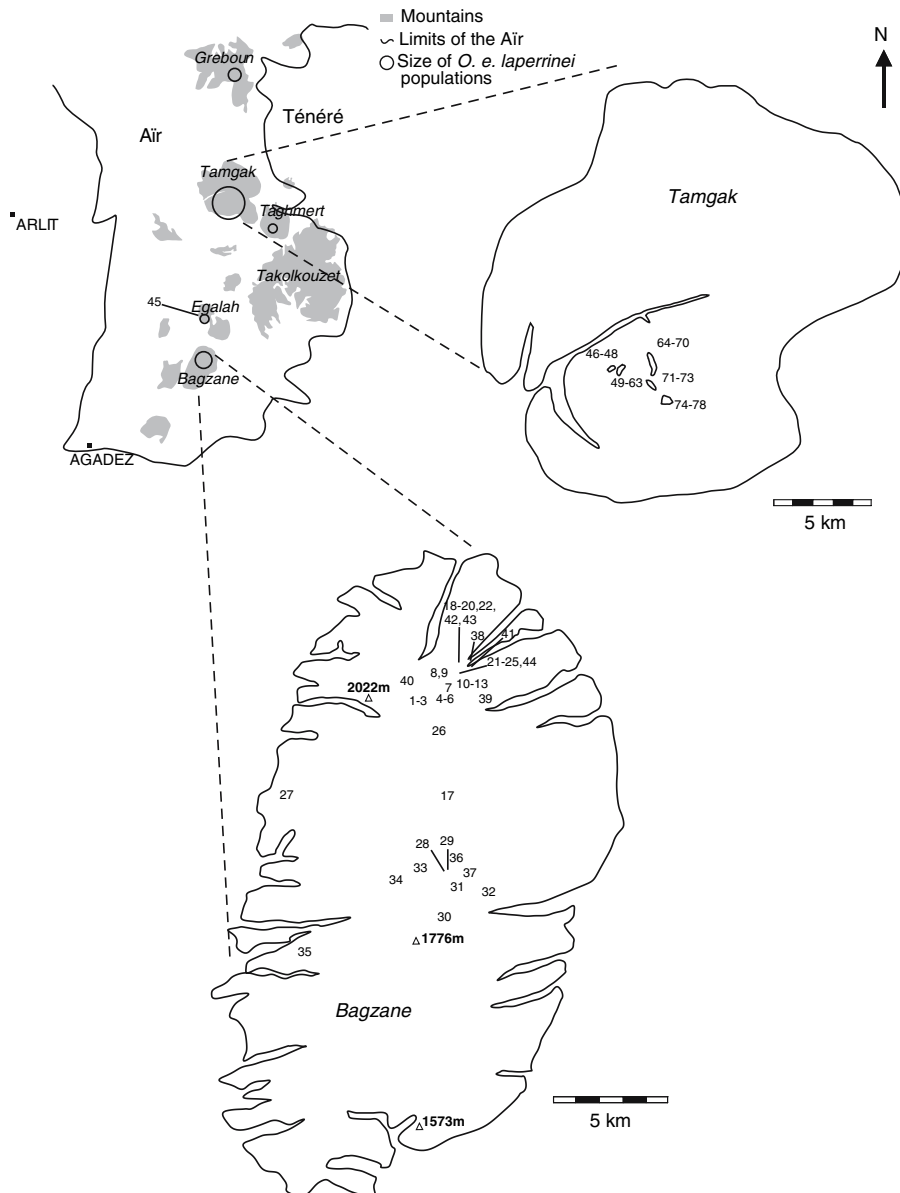


Fig. 2 Distribution and population sizes of *Olea europaea* subsp. *laperrinei* inside the Air mountain range. Focus on the site distribution in the Bagzane and Tamgak mountains ($n = 78$; see Appendix for correspondence between sites and location of trees)

north-eastern corners of the mountain range whereas they increase with elevation (Gallaire 1995). Mean annual temperature at 700 m reaches 26.8°C (Giazzi 1996). On the high plateaux at elevations above 1500 m, temperatures lower than 0°C are not rare in December and January. Soils are lithosols and regosols, often very thin (Giazzi 1996).

The vegetation belongs to three main groups (Poilecot 1996): (i) the inter-mountain vegetation is the richest, supplied with water by the wadis and divided into two large types: the banks of wadis dominated by *Hyphaene thebaica*, *Faidherbia albida*, *Acacia nilotica* subsp. *nilotica* and *Salvadora persica*, and the clay–sand plains dominated by two associated species, *Acacia tortilis* subsp. *raddiana* and *Panicum turgidum* (Anthelme et al. 2007); (ii) the mountain vegetation is distinguished by the introgression of some tropical species that avoid the arid plains, such as *Commiphora africana*, *Acacia laeta*, *Acacia seyal* (Schulz and Adamou 1994), as well as some Saharan mountain species, such as *O. e. laperrinei*, *Lavandula antinae*, *Rumex vesicarius* and *Salvia aegyptiaca*; (iii) the desert vegetation is very poor in species and scarce in the Aïr mountain range. It is composed mostly of hemicryptophytes characteristic of sandy places in the southern Sahara, in particular *Centropodia forskalii*, *Stipagrostis acutiflora* and *S. vulnerans* (Poilecot 1999).

The vegetation cover degrades rapidly under the influence of disturbances caused by human-related activities. This is mainly assignable to the settlement of human populations in the urban centres of Arlit and Agadez (approximately 100,000 inhabitants each; Fig. 1), the intensification and mechanization of irrigated agriculture, and rapid population growth associated with the intensification of livestock farming (Anthelme et al. 2006). The establishment of a Nature Reserve in the eastern half of the Aïr (Fig. 1) has very little effect on the conservation of species and ecosystems because it is very poorly funded. Accordingly, the protection of the biodiversity in general and of *O. e. laperrinei* in particular depends today essentially on the goodwill of local residents and on the distance that separates them from the urban centers (Anthelme et al. 2006). Mountain ecosystems where *O. e. laperrinei* develops are less affected by recent changes because of a low accessibility. As an exception however, the Bagzane ecosystems are already outstandingly degraded and this has been related to the high local

population density associated with free-range livestock farming, by goats essentially (Anthelme et al. 2006). This may constitute a threat for the maintenance of *O. e. laperrinei* populations, as for many other species.

Data collecting and processing

Of the three massifs where *O. e. laperrinei* has been previously described in the Aïr, the sampling was limited to the Bagzane and the Tamgak mountains. In both areas, the presence of *O. e. laperrinei* (in Tamasheq: *Aleo*) was detected through a combination of field observations and surveys among the local residents. Data were collected in August and September 2004 in the Bagzane and in April 2004 in the Tamgak. In addition, the Egalah, a small mountain in the north of the Bagzane, was quickly visited after local inhabitants hypothesized the existence of *O. e. laperrinei* there.

In the Bagzane mountains, sampling of trees was systematic as a result of the low number of individuals present. In the Tamgak mountains, the *O. e. laperrinei* population size was larger and consequently our tree sampling was limited to only one representative zone (Fig. 2; see Appendix for coordinates).

First, we studied vegetative features of *O. e. laperrinei* trees sampled on 78 sites across the massifs of the Bagzane, the Tamgak and the Egalah (Appendix). Trees were subjected to the following measurements: height of the highest stem, maximal length at ground level, circumference of the largest stem (when the tree is multi-stemmed) at 0.5 m above the soil surface, and signs of human-related damages (cuttings, browsing, harvesting, fire).

In order to assess the importance of CG in Niger populations, the genetic profile of each tree was characterized using nuclear DNA markers according to Baali-Cherif and Besnard (2005) by collecting a few leaves on each tree. DNAs were extracted from silica-dried leaves using a CTAB method (Besnard et al. 2000). Nine microsatellites (single strand repeat, SSR) loci were selected (Baali-Cherif and Besnard 2005): DCA1, DCA3, DCA8, DCA9, DCA14, DCA15, GAPI45, PA(ATT)2 and EMO03. Nuclear SSRs were chosen because, they reveal a higher level of polymorphism compared with other genetic markers (Belaj et al. 2003) allowing a robust genotype identification. The probability (P_{gen}) that two sampled trees belonging to different genets would have the

same genotype by chance was calculated according to Parks and Werth (1993). The trees with the same SSR profile, i.e., belonging to the same genet, were called clones (see Results). In addition, each tree generally displayed several stems that were interconnected at ground level (multi-stemmed trees), which was taken as a supplementary index of CG.

Additionally, we characterized the habitat where *O. e. laperrinei* trees were present. Among habitats, the ravines contrast with the hillsides due to the flow of water that is channelled and seasonal. They also contrast with the borders of ‘wadis’ (non-permanent water courses) by the absence of a bed and by much steeper walls. No trees were found on rocky plateaux or clay–sand plains in our sample. The following variables were taken into account: nature of substratum (granitic or volcanic), estimation of the slope gradient, elevation (GPS garmin 12 XL), and geographical coordinates (GPS). Relationships between *O. e. laperrinei* attributes and environmental variables were analyzed (ANOVA and Chi² analyses when specific conditions were met) with Minitab 14 software (Minitab Ltd, Coventry, UK).

Lastly, the presence of trees, shrubs and the most frequent plant species were recorded at each site of *O. e. laperrinei*. Latin binomials for plants fitted those of the Conservatoire Botanique de la Ville de Genève (Database of the Flowering Plants of Africa South of the Sahara 2006).

Results

Size and distribution of populations

A total of 143 trees were recorded: (i) In the Bagzane mountains, we sampled 83 trees belonging to two separate areas, i.e., the northern and central parts of the massif (Fig. 2). Up to now, only the northern area was known to shelter *O. e. laperrinei* in the Bagzane (Bruneau de Miré and Gillet 1956a). O57 and O70 were the only trees located in the eastern area; (ii) In the Tamgak mountains, the presence of about 2000 trees was estimated based on observations of inhabitants. Only 58 trees were sampled in the southern valley of the central part of the massif (“Faille du Tamgak”, Fig. 2); (iii) In the Egalah mountains, where *O. e. laperrinei* was reported for the first time, only two trees (O84 and O85) were found.

Sites of *O. e. laperrinei* ranged from 1550 to 1850 m (Appendix) while the highest point in the two massifs is approximately 2000 m. They were distributed similarly across massifs at a mean elevation of 1704 m (ANOVA: $F = 0.08$, $p \leq 0.773$) and they grew only on a granite substratum.

Characteristics of recorded trees (Table 1)

The height of trees averaged approximately 4 m, ranging from 0.94 m (O132) to 7 m (O76). In parallel, the maximal length of (multi-stemmed) trees at ground level averaged slightly less than 6 m. As a general rule, it followed the direction of the slope gradient, it reached however 20 m for O36 (eight stems). The mean circumference of the thickest stem of trees was 0.61 m, however that of O119 reached 3.84 m, i.e., an estimated diameter of 1 m. No significant difference was detected across the samples from the two massifs with regards to height, maximal length or circumference. Signs of human-related damages, mainly browsing and cutting of branches and/or stems, were found on almost half of the trees. Nevertheless, they were twice more frequent on trees from the Bagzane mountains than on trees from the Tamgak (Pearson Chi² = 6.72, $p \leq 0.01$).

Fruiting was studied on samples from the Bagzane mountains ($n = 81$) and was found to be extremely rare. A few fruits were detected on O25, O26, and O29, i.e., less than 4% of the sampled trees. At the same time, no seedling and/or sapling was observed in either of the two massifs.

Evidence for clonal growth

Among the 133 DNA samples that could be extracted from trees, including two of the Egalah mountains, only 98 different genotype profiles (or genets) were detected (Appendix). The probability of obtaining the same genetic profile by chance (P_{gen}) was negligible, ranging from 7×10^{-5} (O15–O16) to 1×10^{-11} (O62–O63), therefore, two trees with the same SSR profile were considered to correspond to a clone. Additionally, as reported by Baali-Cherif and Besnard (2005), a few cases of somatic mutations leading to three alleles at a locus were identified on trees O84 (DCA9; genotype 179–189–191) and O139 (DCA9; genotype 175–179–181). Additionally, trees

Table 1 *Olea e. laperrinei*'s characteristics in the Bagzane and the Tamgak, mean values with standard errors

	Bagzane ($n = 83^a$)	Tamgak ($n = 58$)	Total
Height of the highest stem (m)	3.78 ± 0.15	4.03 ± 0.15	3.88 ± 0.11
Maximal length at ground level (m)	5.46 ± 0.43	5.99 ± 0.37	5.67 ± 0.29
Circumference of the thickest stem (m)	0.66 ± 0.04	0.55 ± 0.08	0.61 ± 0.04
Trees with human-related damages (%)	61	33	43**
Trees with fruits (%)	3.7	— ^b	— ^b
Juvenile sexual saplings	0	0	0
Genets with two or more clones (%)	40	13	28**
Number of stems per tree	2.92 ± 0.29	4.00 ± 0.32	3.47 ± 0.25

** Chi² test significant at $p \leq 0.01$

^a Except for signs of human-related damages ($n = 31$)

^b Observations outside fruiting period in the Tamgak

O25–O26–O27 surprisingly displayed three alleles at three loci (DCA1; genotype 244–246–254; DCA8; genotype 121–135–139; EMO03; genotype 205–210–218). Such a genetic pattern has recently been revealed in the olive complex for polyploid trees (Besnard et al. [in press](#)) and the diploid status of clone O25–O26–O27 can thus be questioned.

The efficiency of CG was evidenced with 28% of the genets being represented with two or more trees (clones). This ratio was significantly higher in the Bagzane (where it reached 40%) than in the Tamgak (13%; Pearson Chi² = 8.79, $p \leq 0.01$, Table 1). Especially, it was higher than expected in ravines and on hillsides of the Bagzane mountains, unlike on wadi borders. The distance between clones was always less than 15 m, except for O73 with O71 and O72 (Appendix).

The efficiency of CG was also demonstrated by the mean occurrence of 3.47 stems on each tree (Table 1). Single-stemmed trees were scarce (13%) whereas a maximum number of 20 stems differentiated at the ground level were found on tree O84, in the Egalah mountains.

Habitat

The distribution of trees across habitats and massifs was uneven with a deficit of observed sites on the wadi borders of the Bagzane, compared to that of the Tamgak (Table 2).

A single type of trees was observed on wadi borders, with greater height and circumference (Table 3). The vegetation cover on wadi borders

Table 2 Observed (in italic) and theoretical (in regular) distributions of *O. e. laperrinei* genets among massifs and habitats (Pearson Chi-square = 17.12, $p \leq 0.001$)

	Hillsides	Ravines	Wadi borders	Total
Bagzane	<i>21</i>	<i>26</i>	<i>5</i>	<i>52</i>
	17.51	20.69	13.80	52.00
Tamgak	<i>12</i>	<i>13</i>	<i>21</i>	<i>46</i>
	15.49	18.31	12.20	46.00
Total	<i>33</i>	<i>39</i>	<i>26</i>	<i>98^a</i>
	33.00	39.00	226.00	98.00 ^a

^a Genet O87–O88–O89–O90 displayed two habitats (ravine and hillside)

and in ravines was more abundant than that found on hillsides. Lastly, the elevation of the sites located on the wadi borders of the Tamgak ($n = 17$) was higher than that of the sites in the other habitats ($n = 60$; Table 3, Appendix).

Associated species

Among the trees and shrubs, *Rhus tripartita* and *Acacia tortilis* subsp. *raddiana* were the species the most frequently associated with *O. e. laperrinei*. They were similarly distributed in the Bagzane and the Tamgak mountains (Table 4), as well as the tropical trees *Ficus cordata* subsp. *salicifolia*, *Ficus ingens* var. *ingens* and *Boscia salicifolia*. *Dichrosta-chys cinerea*, another tropical tree, was especially frequent in the Bagzane. Among the herbaceous species, the grasses *Cymbopogon schoenanthus* and *Chrysopogon plumulosus* were frequent in the two massifs, whereas *Tripogon multiflorus* was

Table 3 Variance analysis (ANOVA) of the shape and environment of individuals among habitats

<i>n</i>	Hillsides 28	Ravines 32	Wadi borders 17	<i>F</i> -value	<i>p</i>
Height (m)	3.69 ± 0.17	3.59 ± 0.15	4.60 ± 0.21	8.55	***
Circumference (m)	0.55 ± 0.05	0.53 ± 0.04	0.82 ± 0.14	4.58	*
Vegetation cover (%)	36 ± 3	24 ± 3	37 ± 4	4.83	*
Elevation (m)	1697 ± 7		1731 ± 12 ^a	5.30	*

^a Wadi borders of the Tamgak uniquely

*** $p \leq 0.001$; * $p \leq 0.05$

characteristic of the Bagzane. The saharo-mountainous *Lavandula antinae* was present in the Bagzane and the Tamgak at the same time.

Discussion

Distribution of the Laperrine's olive populations in the Air

Our observations confirm those previously made (Bruneau de Miré and Gillet 1956a) on the presence of *O. e. laperrinei* in the Bagzane and Tamgak mountains. A field mission conducted in the spring of 2006 also

Table 4 Occurrence of the most common species associated with *O. e. laperrinei* in the Bagzane and the Tamgak

Species	Bagzane (<i>n</i> = 28)	Tamgak (<i>n</i> = 33)
<i>Acacia tortilis</i> subsp. <i>raddiana</i>	22	28
<i>Acacia ehrenbergiana</i>	+	12
<i>Acacia laeta</i>	+	7
<i>Acacia seyal</i>	+	3
<i>Boscia salicifolia</i>	+	+
<i>Dichrostachys cinerea</i>	20	7
<i>Rhus tripartita</i>	26	30
<i>Carissa edulis</i>	1	0
<i>Commiphora africana</i>	+	0
<i>Ficus cordata</i> subsp. <i>salicifolia</i>	+	+
<i>Ficus ingens</i> var. <i>ingens</i>	+	+
<i>Lavandula antinae</i>	4	9
<i>Chrysopogon plumulosus</i>	22	16
<i>Tripogon multiflorus</i>	18	3
<i>Eragrostis pilosa</i>	19	+
<i>Cymbopogon schoenanthus</i>	15	30
<i>Pachycymbium decaisneanum</i> subsp. <i>decaisneanum</i>	1	0

+: quantitative data not available

confirmed its existence in the Greboun mountains (Morel unpublished data). Aside from these three massifs, the highest in the Air range, *O. e. laperrinei* was identified for the first time in the Egalah mountains and it has recently been reported in the Taghmert mountains, where it was observed by the former chief guide of the Nature Reserve (Tcholli unpublished data). The Laperrine's olive is thus distributed in five different massifs and not three (Fig. 2). It is suggested however that the respective sizes of the populations in the Egalah and the Taghmert mountains are very low (≤ 40 trees each?), given their modest elevation and their limited areas of distribution (Fig. 2).

The identification of a new population in the Bagzane (central zone) also enlarges the distribution area of the Laperrine's olive in the Air mountain range and extends its limit further to the South. The population size in the Bagzane remains nevertheless very low, similarly to the population sizes in the Greboun (Quézel 1962), the Egalah and the Taghmert mountains. It is thus in the Tamgak, in the centre of the Air range, where the largest population of *O. e. laperrinei* is found.

Habitat comparison of the *O. e. laperrinei* populations in the Air, the Hoggar and the western Darfur (Table 5)

A certain number of characteristics observed in the Air mountain range are common to the entire area of distribution of the Laperrine's olive (Table 5). Thus, in all cases, they are located on relief at elevations higher than or equal to 1200 m. In appearance, this tree remains generally bushy even though it can reach considerable heights (i.e., 7 m for tree O76). Finally, it seems that its favourite habitat is on the banks of temporary or permanent water courses (i.e., wadi border and ravine).

Table 5 Respective shapes and environments of the Laperrine’s olive in the Hoggar, the Air, and the western Darfur

Mountain range	Hoggar ^{b,d,e,f,j}						Air		Western Darfur	
	Tassili n’Immidir	Tefedest	Tassili n’Ajjer	Atakor ^a	Greboun ^c	Tamgak	Bagzane	Jebel Gourgeil ^{g,h}	Jebel Marra ⁱ	
Highest summit (m)	1684	2336	2254	2918	1944	1988	2022	2397	3088	
Species altitudinal range (m)	1300–2700 ^b				1550–1900	1400–1820	1550–1850	1700–2200	2300–3000	
Rainfalls (mm yr ⁻¹)	30–150 ^{c,d}				50?	100?	170	500	800–1000	
Substratum	?	Granite	Sandstone/ Granite/ Volcanic	Granite/ Volcanic	Granite ^k	Granite	Granite	Gneiss/Granite/ Volcanic?	?	
Habitat	Ravines/Rocky wadi borders	Ravines/Rocky wadi borders	Ravines/Rocky wadi borders of pools	Ravines/ Rocky wadi borders	Ravines	Ravines/ Hillsides/ wadi borders	Ravines/ Hillsides/ Wadi borders	Rocky hillsides/ Shaded hillsides	Plateaux/ Hillsides/ Borders of streams (best habitat)/ Ravines	
Population size	Small ^e	Large ^d	Medium ^d	Large ^d	Small (50)	Medium	Small	Large	Large?	
Sexual reproduction efficiency	None ^d				None	None	None	Efficient	Efficient	
Vegetative growth	Predominant multi-stemmed trees ^f				Predominant multi-stemmed trees			?	?	
Height (m)	3–6 ^b				?	4, up to 6	4, up to 7	6–8 up to 15	Up to 12	
Vegetation cover (%)	60–100 ^j				?	30–40	30–40	50–90	80–100 (meadow)	
Human impact	High ^b				?	Medium	High	High	Very high	

^a Often called Hoggar itself; ^bSahki and Sahki (2004); ^cQuézel (1962); ^dQuézel (1965); ^eBenichou (1962); ^fQuézel (1962); ^gQuézel (1969); ^hWhite (1983); ⁱWickens (1976); ^jQuézel (1954); ^kMorel unpublished data

However, with regards to certain aspects, the populations found in the Air demonstrate distinctive characteristics explaining in part the small size and the fragmentation of its populations (Table 5). First, annual precipitations in the Air mountains, reaching 170 mm year^{-1} in 2004–2005, like those in the Hoggar, are far weaker than those in the western Darfur (Table 5). Consequently, *O. e. laperrinei* in the Air and the Hoggar is restricted where water is available, i.e., wadi borders, ravines and hillsides, whereas it grows in very diverse habitats in the Darfur, including plateaux.

Unlike in the Hoggar however, the highest elevation in the Air is relatively low (2022 m), providing only a narrow altitudinal range of approximately 300 m for *O. e. laperrinei* to develop. Moreover, whereas the Hoggar is shaped with large massifs (Fig. 1), the Air displays small and isolated massifs in a matrix of low valleys where *O. e. laperrinei* cannot grow (Fig. 2). These multiple constraints act negatively on the size of populations but also on the habitats of *O. e. laperrinei*. Especially, the populations of the Air grow only on granite substratum, which provides better hydric conditions than volcanic substratum. In contrast, populations of the Hoggar grow on both substrata, giving birth to two distinct types of vegetation communities (Quézel 1965; Table 5).

Associated vegetation in the Hoggar is nevertheless different from that of the Air, as most of the characteristic species (*Stipa* spp., *Crambe kralikii*, *Pistacia atlantica*) were not found in the Niger mountains. A substantial exception was the occurrence of *Rhus tripartita*, found frequently in granitic habitats in both mountains. In turn, *Dichrostachys cinerea* is a regular companion of *O. e. laperrinei* in the Air and the western Darfur (Quézel 1969; Wickens 1976) and is the most frequent representative of a pool of tropical species shared by these mountain ranges.

As a consequence, *O. e. laperrinei* in the Air presents unique characteristics. Sharing the aridity of the Hoggar, it displays a similar multi-stemmed short shape (Table 5) but sharing the tropical influence with the western Darfur, it displayed similarities with associated vegetation. Most of all, it is restricted to very small and fragmented areas that make it particularly sensitive to environmental changes.

Impact of human-related activities

The Bagzane mountains, located more in the South than the Tamgak mountains, present a water balance that is more favorable from rainfall and edaphic points of views owing to the presence of clay–sand plateaux (e.g., Ingram 1990). However, the Laperrière's olive is much less frequent there and has a tendency to colonize hillsides and ravines, which are inaccessible for people, rather than wadi borders, which provide more favorable conditions in a Saharan context (Quézel 1965) as is attested by the presence of taller trees in these habitats. This deficit is correlated with the ancient presence of settled populations on the Bagzane (Adamou and Morel 2005), which has had a much more significant impact than in the Tamgak mountains (Ingram 1990). It demonstrates that the human-related activities seem to have played an important role in the distribution of *O. e. laperrinei* in the Air, as it was shown in the Hoggar (Sahki and Sahki 2004) and the western Darfur (Quézel 1969; Wickens 1976; White 1983). Together with the current hyper-arid climatic period, they constitute a serious constraint for the development of *O. e. laperrinei*, especially expressed through a current lack of sexual reproduction.

Prevailing strategy of clonal growth

As a result of a defective sexual reproduction for both climatic and anthropogenic reasons, as in the Hoggar (Baali-Cherif and Besnard 2005) but not in the Darfur (Wickens 1976), the Air populations tend to become remnant populations *sensu* Honnay and Bossuyt (2005), using CG as a strategy of long-term persistence in a harsh environment that does not allow it to complete the normal life cycle. Its efficiency, represented through the ratio of genets represented by more than one tree, is high in comparison with other shrub species for which CG is a prevailing strategy of regeneration (e.g., 16% for *Spartocytisus supranubius*; Kyncl et al. 2006). An interesting point of view is to match this ratio with the respective sizes of populations. The smallest population displayed the highest CG (Bagzane, 83 trees, CG = 40%) before the Tassili n'Ajjer (CG = 26%; Besnard et al. *in press*), the Tamgak (about 2000 trees, CG = 13%), and the Atakor (where several thousands of trees are

present, CG = 14%; Besnard et al. [in press](#)). While facing relatively comparable aridity (e.g., Ozenda 2004), this variability in population size between the Tamgak and the Bagzane is interpreted as a response to a gradient of a pool of other environmental constraints (area availability, isolation, impact of human-related activities, habitat fragmentation) along which CG is increasingly used by *O. e. laperrinei*.

In conservation terms, CG is interesting but it has a substantial cost. In one hand, it gives a potential long-term persistence to small-sized populations (Eriksson and Ehrlén 2001) especially because clones are less affected by browsing since shoots are more resistant than seedlings (Kyncl et al. 2006). In that case, regeneration is provided either with clonal-splitting strategy (Schenk 1999) or through integrator strategy, i.e., when trees keep interconnected and optimize the distribution of resources (Oborny et al. 2001; see the multi-stemmed characteristics of the trees). Long-term persistence of trees also slows down loss of genetic diversity through genetic drift (Young et al. 1996), which can become problematic with a high habitat fragmentation and a small population size (e.g., Richards 2000). But in the other hand, clonal populations should be more sensitive to stochastic events, like the proliferation of a pathogen agent (Honnay and Bossuyt 2005). It could also lead to sexual extinction *sensu* Honnay and Bossuyt (2005) because of successive mutations making genets not compatible at last (Klekowski 1997).

Altogether, the structure of *O. e. laperrinei* populations demonstrates that the current strategy for persistence within a hyper-arid context coupled with a human-related disturbance (browsing and cutting) is the CG. However, the occurrence of 98 different genets and the relatively short distance between trees demonstrates in all likelihood the former occurrence of a seeding phase, probably triggered during a less arid period as currently observed in the Jebel Marra (Wickens 1976). Adding to the fact that the age of trees in the Aïr mountain range has been estimated up to 2000 years (Quézel 1965), these results fit the model of multiple demographic strategies in arid and semi-arid environments, which states that CG coupled with longevity becomes a strategy of persistence in stressful environments, whereas periods of sexual regeneration take place when environmental constraints decrease (Garcia and Zamora 2003). To complete the model, we should

add that disturbance, mainly represented here by browsing, is an important factor of strategy alternation (see also Kyncl et al. 2006).

Long-term conservation?

Even though the populations of *O. e. laperrinei* are distributed in several massifs in the Aïr, they generally display a very small size (notably in the Bagzane mountains as probably in the Greboun, the Egalah and the Taghmert). As a consequence of the genetic drift and a limitation of gene flow at long distance, the genetic differentiation between Niger populations is relatively high when compared to southern Algerian mountains (Besnard et al. [in press](#)). Our demographic observations also sustain that the main centres of distribution of the Laperrière's olive are the Hoggar and the western Darfur. Even more than the current absence of sexual reproduction (which is temporarily compensated by clonal growth), interactions with human populations is a determining factor in the conservation of the Laperrière's olive in Niger where its limited distribution makes it more vulnerable than in all the other mountain ranges.

A long-term monitoring of the populations of the Laperrière's olive is today discussed in order to understand more precisely the nature of its interactions with people. They could be positive, for example through the sacred nature of rare or old trees as in the Egalah mountains or the Darfur (Wickens 1976), thus demonstrating the value of integrating local people into the conservation movement (McNeely 2003). Monitoring would also allow determining whether, during the course of a more favorable rainfall cycle, sexual reproduction could be triggered as in the Jebel Marra (Wickens 1976). It would certainly be relevant as well to test the hypothesis that human-related activities are the main factor of extinction of *O. e. laperrinei* in the mountain chains of the Ennedi and the Tibesti, which, as in the Aïr, are the biogeographical links between the Hoggar and the western Darfur.

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Appendix Distribution of sites ($n_{\text{site}} = 78$), trees ($n_{\text{tree}} = 143$) and genets ($n_{\text{genet}} = 98$) across the massifs of the Bagzane (B), the Tamgak (T), and the Egalah (E). Coordinates expressed in UTM (32Q)

Massif	Site	Trees	Habitat	Latitude	Longitude	Elevation (m)	[Clones] and missing data
B	1	O1	Hillside	473815	1972072	1728	[O1]
B	2	O2	Wadi border	473848	1972145	1712	[O2]
B	3	O3	Hillside	473920	1972251	1729	[O3]
B	4	O4–O5	Hillside	474775	1972259	1735	[O4–O5]
B	5	O6–O8	Ravine	474874	1972184	1703	[O6–O7] and [O8]
B	6	O9–O16	Ravine	474878	1972245	1750	[O9–O10–O11], [O12], [O14] and [O15–O16]; O13 missing
B	7	O17–O18	Hillside	474895	1972425	1755	[O17–O18]
B	8	O19	Hillside	475253	1973412	1770	[O19]
B	9	O20–O21	Hillside	475258	1973360	1775	[O20] and [O21]
B	10	O22–O23	Ravine	475669	1973221	1765	[O22–O23]
B	11	O24	Hillside	475582	1973244	1755	[O24]
B	12	O25–O28	Hillside	475567	1973319	1755	[O25–O26–O27] and [O28]
B	13	O29	Ravine	475501	1973365	1708	[O29]
B	14	O30–O31	Hillside	475503	1973370	1719	[O30–O31]
B	15	O32	Ravine	475482	1973445	1730	[O32]
B	16	O33–O34	Ravine	475477	1973491	1743	[O33–O34]
B	17	O35–O36	Ravine	474665	1966170	1710	O35 and O36 missing
B	18	O37–O39	Ravine	475635	1973595	1731	[O37–O38] and [O39]
B	19	O40	Ravine	475848	1973633	1740	[O40]
B	20	O41–O44	Ravine	475724	1973687	1741	[O41], [O42] and [O43–O44]
B	21	O45, O50–O51	Hillside	475910	1973830	1688	[O45] and [O50–O51]
B	22	O46	Ravine	475759	1973604	1677	[O46]
B	23	O47–O49	Hillside	475920	1973846	1705	[O47–O48] and [O49]
B	24	O52–O53	Ravine	475948	1973847	1691	[O52] and [O53]
B	25	O54	Wadi border	475879	1973862	1670	[O54]
B	26	O55–O56	Ravine	475159	1970217	1780	[O55–O56]
B	27	O57	Ravine	464741	1966528	1658	O57 missing
B	28	O58–O59	Hillside	475060	1960837	1800	[O58]; O59 missing
B	29	O60–O61	Hillside	474938	1960809	1690	[O60–O61]
B	30	O62–O63	Ravine	474172	1958868	1617	[O62–O63]
B	31	O64	Ravine	475365	1960146	1580	[O64]
B	32	O65–O66	Ravine	477188	1960310	1595	[O65–O66]
B	33	O67	Hillside	472944	1961647	1550	[O67]
B	34	O68–O69	Hillside	471455	1961027	1628	[O68–O69]
B	35	O70	Ravine	465698	1956417	1672	[O70]
B	36	O71–O72	Ravine	475454	1961336	1677	[O71–O72–O73]
B	37	O73	Ravine	476152	1961101	1638	
B	38	O74	Hillside	476438	1974255	1620	[O74]
B	39	O75	Wadi border	477274	1972323	1624	[O75]
B	40	O76–O78	Wadi border	472046	1973423	1662	[O76–O77–O78]
B	41	O79	Ravine	476436	1973873	1850	[O79]
B	42	O80–O81	Hillside	475620	1973517	1622	[O80–O81]
B	43	O82	Hillside	475726	1973610	1710	O82 missing

Appendix continued

Massif	Site	Trees	Habitat	Latitude	Longitude	Elevation (m)	[Clones] and missing data
B	44	O83	Wadi border	475791	1973819	1765	[O83]
E	45	O84–O85	Ravine	–	–	–	[O84–O85]
T	46	O86	Hillside	460065	2106994	1641	[O86]
T	47	O87–O89	Ravine	460094	2106987	1645	[O87–O88–O89–O90]
T	48	O90–O91	Hillside	460108	2106983	1648	[O91]
T	49	O92–O93	Hillside	460961	2107141	1637	[O92–O93]
T	50	O94	Hillside	460951	2107088	1640	[O94]
T	51	O95	Ravine	460893	2107103	1635	[O95]
T	52	O96	Ravine	460868	2107046	1653	[O96]
T	53	O97	Hillside	460876	2106936	1682	[O97]
T	54	O98–O99	Ravine	460798	2106954	1688	[O98–O99]
T	55	O100	Hillside	460786	2106944	1692	[O100]
T	56	O101–O102	Ravine	460754	2106906	1701	[O101] and [O102]
T	57	O103–O106	Ravine	460752	2106886	1704	[O103–O104], [O105] and [O106]
T	58	O107	Ravine	460742	2106847	1711	[O107]
T	59	O108	Hillside	460775	2106815	1712	[O108]
T	60	O109	Hillside	460839	2106833	1702	[O109]
T	61	O110	Ravine	460829	2106850	1701	[O110]
T	62	O111–O112	Hillside	460857	2106878	1693	[O111] and [O112]
T	63	O113	Ravine	460861	2106934	1684	O113 missing
T	64	O114	Ravine	463908	2107561	1708	[O114]
T	65	O115–O116	Ravine	463946	2107527	1716	[O115–O116]
T	66	O117–O122	Wadi border	464282	2107104	1792	[O117–O118–O119], [O120], [O121] and [O122]
T	67	O123–O125	Wadi border	464309	2107055	1802	[O123] and [O125]; O124 missing
T	68	O126	Wadi border	464263	2107215	1767	[O126]
T	69	O127–O128	Wadi border	464263	2107282	1752	[O127] and [O128]
T	70	O129–O132	Wadi border	464253	2107342	1810	[O129] and [O130]; O131 and O132 missing
T	71	O133	Wadi border	463390	2105462	1716	[O133]
T	72	O134	Hillside	463544	2105184	1725	[O134]
T	73	O135	Wadi border	463790	2104947	1740	[O135]
T	74	O136–O138	Wadi border	464624	2103950	1757	[O136], [O137] and [O138]
T	75	O139	Wadi border	464853	2103619	1698	[O139]
T	76	O140–O141	Wadi border	464904	2103597	1697	[O140] and [O141]
T	77	O142	Wadi border	464958	2103565	1738	[O142]
T	78	O143	Wadi border	464517	2103782	1729	[O143]

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