



Putative glacial refugia of *Cedrus atlantica* deduced from Quaternary pollen records and modern genetic diversity

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ABSTRACT

Aim To investigate the impact of past environmental changes on *Cedrus atlantica* and its current genetic diversity, and to predict its future distribution.

Location Morocco, Algeria and Tunisia.

Methods Eleven fossil pollen records from these three countries were used to locate putative glacial refugia and to reconstruct past climate changes. A mechanistic vegetation distribution model was used to simulate the distribution of *C. atlantica* in the year 2100. In addition, a genetic survey was carried out on modern Moroccan *C. atlantica*.

Results Pollen records indicate that *Cedrus* was present during the last glacial period, probably in scattered refugia, in Tunisia, Algeria and Morocco. In the Tunisian and Algerian sites, cedar expanded during the late glacial and the early Holocene, then disappeared after c. 8000 yr BP. Reconstructed mean annual precipitation and January temperature show that the last glacial period in Morocco was cooler by 10–15°C and drier by c. 300–400 mm year⁻¹ than the climate today. Modern chloroplast microsatellites of 15 *C. atlantica* populations in Morocco confirm the presence of multiple refugia and indicate that cedar recolonized the Moroccan mountains fairly recently. Model simulation indicates that by the year 2100 the potential distribution of *C. atlantica* will be much restricted with a potential survival area located in the High Atlas.

Main conclusions Environmental changes in northern Africa since the last glacial period have had an impact on the geographical distribution of *C. atlantica* and on its modern genetic diversity. It is possible that by the end of this century *C. atlantica* may be unable to survive in its present-day locations. To preserve the species, we suggest that seedlings from modern *C. atlantica* populations located in the High Atlas mountains, where a high genetic diversity is found, be transplanted into the western High Atlas.

Keywords

Cedar, *Cedrus atlantica*, DNA, glacial refugia, Northern Africa, phylogeography, vegetation model.

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INTRODUCTION

During the last 20 thousand years (20 kyr), the global climate experienced a change from a glacial climate to one warmer and more humid than that at present. In the temperate Northern Hemisphere, the climate of the last glacial period restricted the

geographical distributions of trees to isolated populations that survived in a few climatically suitable refugia (Willis & van Andel, 2004; López de Heredia *et al.*, 2007; Muller *et al.*, 2007; Bhagwat & Willis, 2008; Magri, 2008). The locations of refugia for many temperate broadleaf and conifer species are now well documented from Quaternary fossil records (e.g. Bennett

et al., 1991; Tzedakis, 1993; Willis, 1994; Carrión, 2002; Tzedakis *et al.*, 2002; Cheddadi *et al.*, 2006).

Past climate change and the spatial distribution of related species have left their imprint in the genetic structure and diversity of populations (Petit *et al.*, 1997, 2005), and it is necessary to integrate genetic and environmental data in order to assess the phylogeography of species and to understand their recent history (Magri *et al.*, 2007), particularly the impact of past changes on their modern genetic diversity (Fady, 2005). During the past decade, in addition to efforts made by the palaeoecological community to reconstruct past distributions of plants during the last glacial period, geneticists have developed cytoplasmic molecular markers (chloroplast and mitochondrial DNA) to describe the genetic structure of extant species. The origin of the genetic diversity of several European forest species is located in areas that played a role as glacial refugia (Petit *et al.*, 2003). The locations of these refugia differed from one glacial period to another, which led to different post-glacial dynamics and ecosystem compositions (Cheddadi *et al.*, 2005; de Beaulieu *et al.*, 2006). Some Mediterranean areas have served as refugia for plants during several climatic cycles (e.g. Greece; Tzedakis *et al.*, 2002). Thus, the current genetic structure of some Mediterranean plant taxa reflects genetic divergence that pre-dates the onset of the Mediterranean climate (Petit *et al.*, 2003), which took place around 2 Ma (Suc, 1984). The history of the genetic diversity of Mediterranean species such as *Quercus ilex* and *Pinus pinaster* can be traced back several millions of years (Magri *et al.*, 2007).

Mediterranean species have adjusted their geographical distributions following the climate oscillations between glacial and interglacial periods since the Tertiary. The impact of past environmental change on the modern genetic diversity of many emblematic Mediterranean tree species, such as *Cedrus atlantica* (Endl.) Manetti ex Carrière, is not well documented. The following question arises: where were *Cedrus* populations during the last glacial period and what was the impact of the post-glacial climate change on their genetic diversity?

The aim of the present work is to evaluate the impact of environmental change since the last glacial period on the modern genetic diversity of *C. atlantica*, by combining palaeoecology, genetics and a mechanistic model that simulates potential distributions of the species. The integration of these three disciplines will, we hope, produce inferences about the potential genotypes best adapted to future climate changes.

EVOLUTION AND BIOGEOGRAPHY OF THE GENUS *CEDRUS*

The genus *Cedrus* currently has a very patchy distribution in northern Africa (Fig. 1a), the Eastern Mediterranean and the western Himalaya (Quézel & Médail, 2003). Genetic data indicate that Tertiary migrations into the Mediterranean of taxa originating in Asia have left their imprint in the modern genetic structure (Qiao *et al.*, 2007). Bou Dagher-Kharrat *et al.* (2007) and Qiao *et al.* (2007) have shown that the Himalayan

cedar, *Cedrus deodara*, diverged first, and then the North African species *C. atlantica* separated from the common ancestor of *C. libani* and *C. brevifolia*. The latter two species are now located in the Eastern Mediterranean region. Qiao *et al.* (2007) used a molecular clock to estimate the timing of the genetic split between *C. atlantica* and the two Eastern Mediterranean species: this split occurred much earlier (c. 25 Ma) than the split between *C. libani* and *C. brevifolia* (c. 8 Ma), which show a strong genetic similarity (Bou Dagher-Kharrat *et al.*, 2007). These authors concluded that it is very likely that *Cedrus* migrated into North Africa in the very late Tertiary.

MODERN DISTRIBUTION OF *CEDRUS ATLANTICA*

To determine the modern geographical distribution of *C. atlantica* (Fig. 1a) we combined information from several maps of its natural distribution (Emberger, 1939; Quézel, 1980; Deil, 1988; Farjon, 1990; M'herit, 1994) with field data gathered using GPS. Today, cedar forests cover an area of over c. 130,000 ha distributed in Morocco (Rif, Middle Atlas and north-east of the High Atlas) and Algeria (Aurès, Belezma, Hodna, Djebel Babor, Djurdjura, Blida and Ouarsenis). *Cedrus atlantica* occurs at elevations between c. 1300 and 2600 m a.s.l., where the amount of annual rainfall ranges from c. 500 to 2000 mm and the minimum temperature of the coldest month is between c. -8 and -1°C (Benabid, 1994). Although it has relatively wide tolerances with regard to climate and soil type, *C. atlantica* is threatened by global warming, particularly by the projected increase of winter temperatures, which will affect soil evaporation and plant evapotranspiration.

PALAEODATA SYNTHESIS IN NORTHERN AFRICA

Unlike temperate regions, northern Africa has few peat bogs, mires or lakes where fossil biological indicators might be well preserved within continuous Quaternary records. Holocene vegetation changes have, however, been documented from pollen data (Reille, 1976, 1977; Ben Tiba & Reille, 1982; Ballouche & Damblon, 1988; Lamb *et al.*, 1989, 1995, 1999; Salamani, 1991, 1993; Lamb & van der Kaars, 1995).

In Morocco, west of the Rif mountains, the pollen diagram of Daya Abartete shows that *Cedrus* (Fig. 2) was clearly present from the beginning of the record (Reille, 1977). This pollen record is not dated but, according to the author, it may span approximately the last 8000 years. Other pollen records confirm that *Cedrus* was present during the Holocene in most of the western part of the Rif (Reille, 1977). However, these records are also poorly dated, which means that it is not possible to reconstruct either the timing of the spread of *Cedrus* or the locations of any potential glacial refugia. In the Middle Atlas, the well-dated pollen records from Lake Tigalmamine (Lamb *et al.*, 1995) and Lake Sidi Ali (Lamb *et al.*, 1999) consistently show that cedars initially spread after

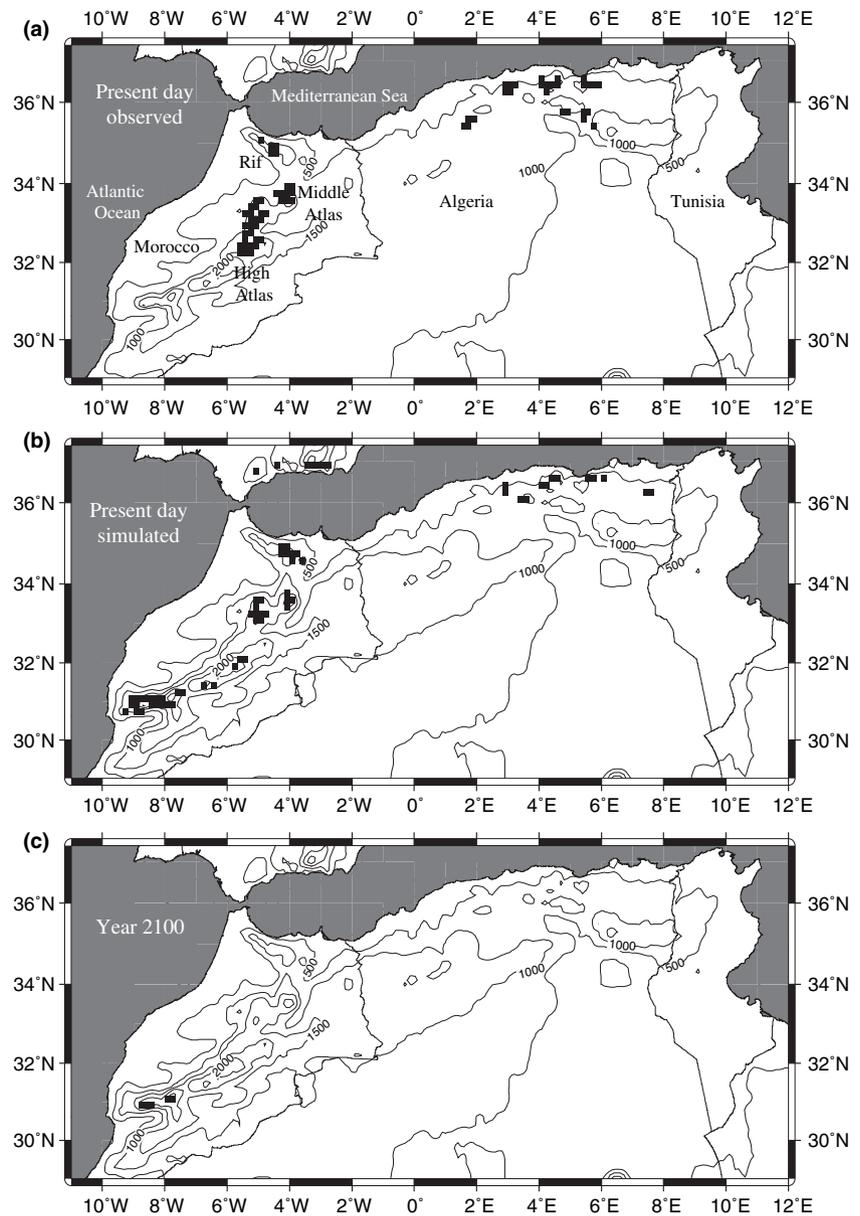


Figure 1 Geographical distribution of *Cedrus atlantica* in northern Africa: (a) modern observed distribution; (b) simulated modern distribution using the CARAIB vegetation model; (c) simulated distribution for the year 2100.

6500 yr BP, and then expanded further after 4500 yr BP (Fig. 2). In the Rif, cedar pollen percentages from Daya Abartete and Tiziren (Reille, 1977) show an opposite trend (Fig. 2). In the pollen record of Tizi n'Inouzane (Reille, 1976), located in the transition between the High and the Middle Atlas (Fig. 2), cedar pollen is present but in very small amounts. Given the scarce fossil evidence, do these pollen percentages correspond with the southern limit of cedar during the Holocene?

During the spring of 2000, a 9-m core was obtained from the edge of Lake Ifrah, Middle Atlas, using a modified Livingstone piston corer. The chronological time frame was inferred from four ^{14}C dates (Table 1). The time span covered by the Ifrah record extends from c. 25 to c. 5 ka. The pollen record (Fig. 3) shows that cedar populations survived in the area during the last glacial period into the mid-Holocene. Between 19 and

16 ka, *C. atlantica* expanded substantially and then it regressed towards the early Holocene, when oak forests began to expand. Other pollen records from the Middle Atlas (Lamb & van der Kaars, 1995; Lamb *et al.*, 1995, 1999) indicate that, during the early Holocene, oak forests dominated the landscape, and *Cedrus* expanded only after 6.5 ka. The Ifrah pollen record is in agreement with these data. The uppermost part of the sequence is probably dated between 5 and 4 ka. Thus, *C. atlantica* was in the area during the past 20 ka and, as observed in two other pollen records from the Middle Atlas (Lake Tigalmamine and Lake Sidi Ali), it retreated during the early Holocene.

In Algeria, one of the most detailed studies for the Late Quaternary is the Chataigneraie site (Salamani, 1993), located in the Massif de l'Akfadou (Great Kabylie). The pollen record covers approximately the last 11,000 years. Cedar dominates

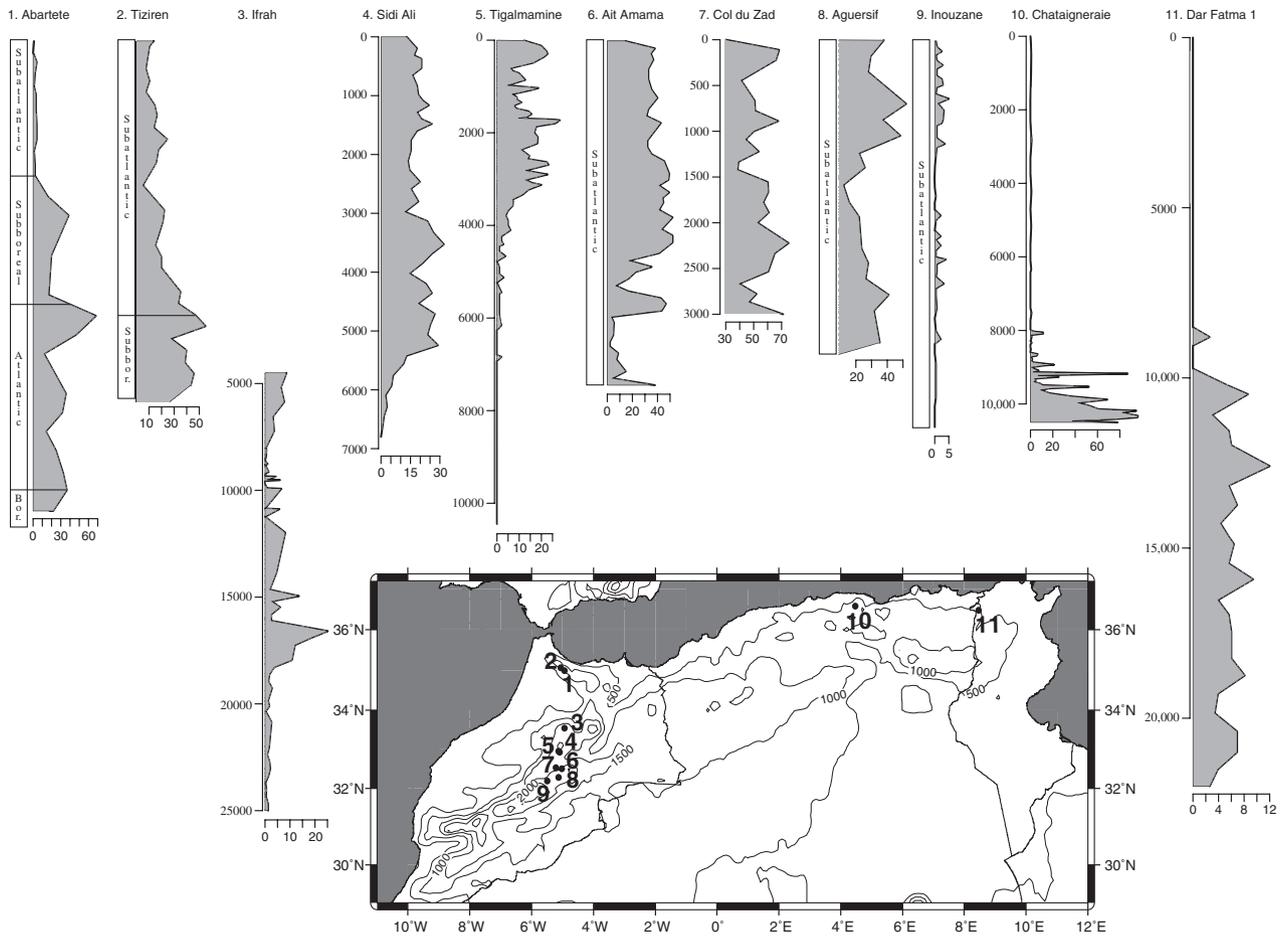


Figure 2 Pollen percentages of *Cedrus* and locations of the corresponding sites. A time frame is applied to those records with available ¹⁴C dates: Lake Ifrah, Lake Sidi Ali, Lake Tigalmamine, Col du Zad, Chataigneraie and Dar Fatma 1. The Holocene chronology of the other records (Abartete, Tiziren, Ait Amama, Aguersif and Inouzane) follows Reille (1976, 1977). Boreal (Bor.): c. 10 ka to 8 ka [11500–8900 calibrated years before present (cal. yr BP)]; Atlantic: c. 8–5 ka (8900–5700 cal. yr BP); Subboreal (subbor.): c. 5–2.5 ka (5700–2600 cal. yr BP); and Subatlantic, c. 2.5 ka to present.

Table 1 List of ¹⁴C-dated samples from the Lake Ifrah record.

Sample	Label	Depth (cm)	Age (¹⁴ C yr BP)
IFR-01	Poz-7469	119–111	8420 ± 50
IFR-03	Poz-7471	320–310	16330 ± 100
IFR-04	Poz-7472	508–500	19430 ± 100
IFR-05	Poz-7473	628–620	20930 ± 120

the base of the record, until c. 9000 yr BP, and declines between 9000 and 8000 yr BP (Fig. 2).

In Tunisia, the pollen records of Dar Fatma (1 and 2) in Kroumirie cover the longest period of time in the Maghreb (Ben Tiba & Reille, 1982). Despite the presence of some sedimentary hiatuses, the Dar Fatma 1 record (Fig. 2) seems to cover most of the last glacial period and shows the presence of cedar until the early Holocene. Although the period of glacial maximum is partly missing from the record of Dar Fatma 2 (Ben Tiba & Reille, 1982), north-east Tunisia possibly also served as a glacial refugium for cedar.

CLIMATE CHANGE SINCE THE LAST GLACIAL PERIOD

In order to analyse the potential impact of past climate change on cedar populations we reconstructed two climate parameters, namely January temperature (T_{jan}) and annual precipitation (Pann), from two pollen records, namely Lake Ifrah and Chataigneraie (Fig. 4). The climate data for Lake Tigalmamine were obtained from Cheddadi *et al.* (1998). These three records span the most extended time period among the 11 records used in this study.

The climate quantification method used is based on the closest modern analogues for each fossil pollen spectrum in a large set of surface samples. In order to be able to discuss the relationship between climate and *C. atlantica* while at the same time avoiding circular reasoning, we removed cedar pollen percentages from both the modern and the fossil pollen samples. The approach and the modern pollen data set used in northern Africa are the same as in Cheddadi *et al.* (1998). The best match between the modern and the fossil samples is

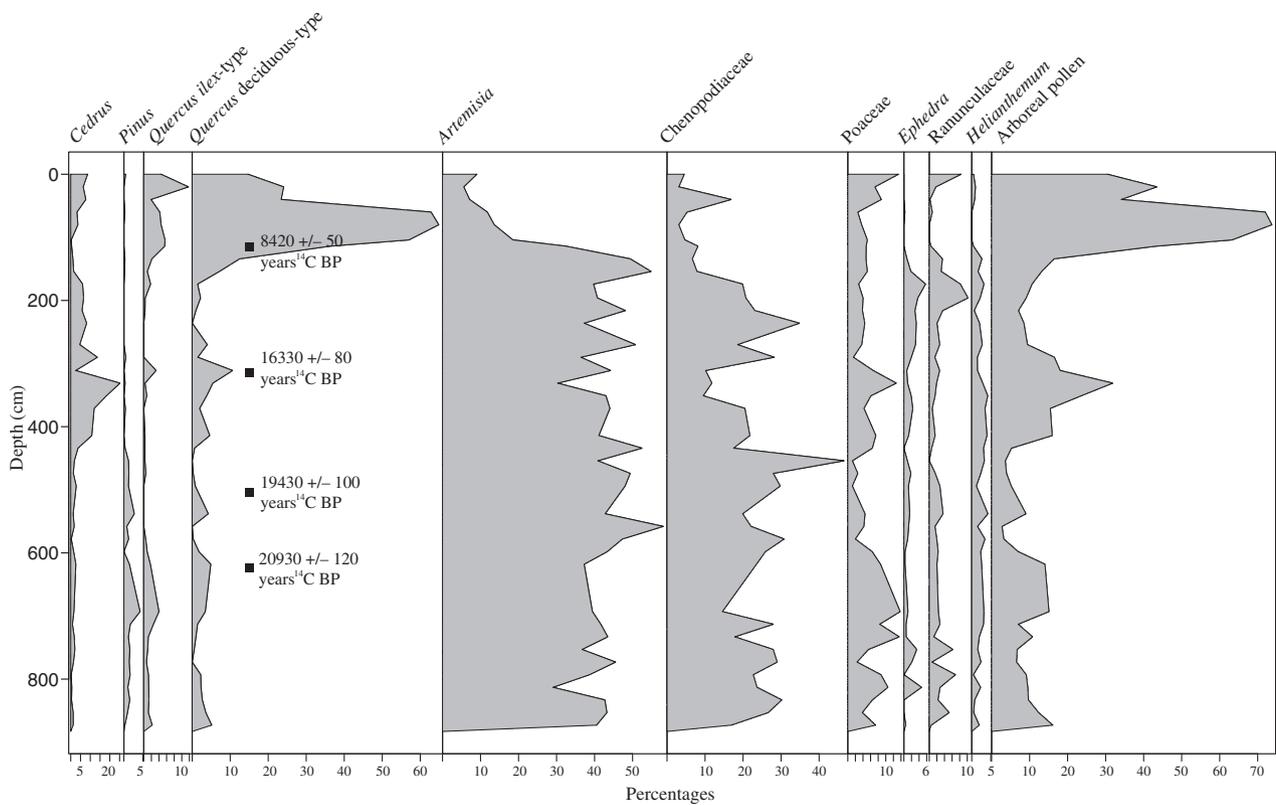


Figure 3 Summary pollen diagram from Lake Ifrah showing the main pollen taxa and four ¹⁴C dates.

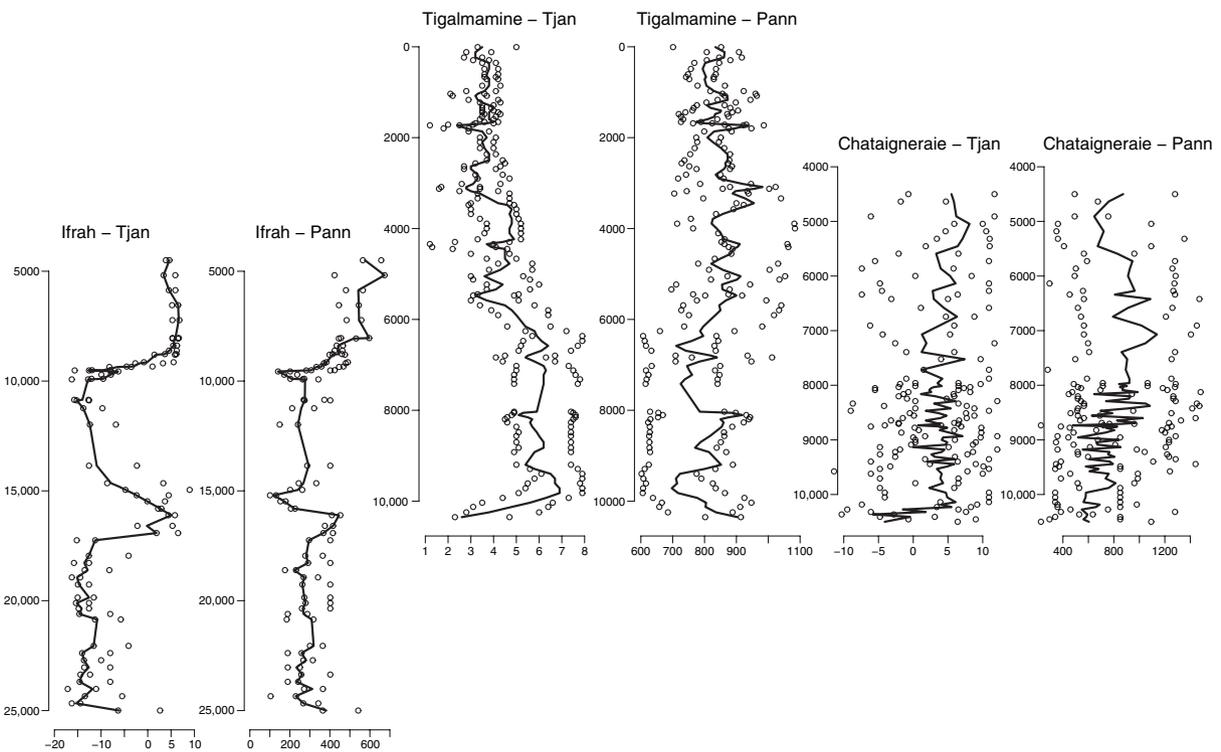


Figure 4 Reconstructed January temperature (Tjan, °C) and annual precipitation (Pann, mm) from Lake Ifrah, Lake Tigalmamine and Chataigneraie. The solid lines are the weighted mean values. The circles above and below each mean value correspond to the standard deviations. The time scale is in radiocarbon years BP.

obtained using the chord distance, which measures the degree of dissimilarity (Guiot, 1990). The procedure followed was to select a few modern analogues (eight maximum) and then use their climate values to compute the mean and standard deviation for each climate variable for all fossil samples.

In Morocco, *Cedrus atlantica* occurs today only in areas where the mean January temperature is below +5°C, even though the amount of annual rainfall might be as low as 500 mm year⁻¹ (Cheddadi *et al.*, 1998). The pollen record from Lake Ifrah shows that *Cedrus* expanded between 19 and 16 ka, when annual precipitation and January temperature increased from 300 to *c.* 500 mm year⁻¹ and from *c.* -12 to *c.* 3°C, respectively (Fig. 4). Reconstructed January temperature and annual precipitation for Lake Tigalmamine (Cheddadi *et al.*, 1998) were above 5°C and above 700 mm year⁻¹ from *c.* 10 ka until 6.5 ka (Fig. 4). *Cedrus* expanded around Lake Tigalmamine only after 6.5 ka.

In Algeria, the reconstructed climate from the Chataigneraie pollen record shows that January temperature was slightly lower than 5°C during the early Holocene and increased after 8 ka (Fig. 4). *Cedrus* was present at the Chataigneraie site until 8 ka.

GENETIC STRUCTURE

Phylogeographic studies have clearly shown that isolated populations of tree species in glacial refugia tend to diverge genetically (e.g. Petit *et al.*, 1997). Genetic diversity between and within populations of the same species can be studied using modern DNA. To investigate the genetic relationship between distinct populations of *C. atlantica* in Morocco we used chloroplast microsatellites (Fady *et al.*, 2003, 2008). Leaf samples were collected from an experimental site of trees grown from seeds collected in natural populations in Morocco (Table 2). Total genomic DNA extraction and polymerase chain reaction (PCR) amplifications were carried out following

Fady *et al.* (2008). The forward PCR primer in each reaction was IRD (infrared fluorescence dye)-labelled, and genotyping was performed using a LI-COR LongReadir 4200 automatic sequencer (Li-Cor Biosciences, Lincoln, NE).

We estimated two genetic diversity parameters: haplotype diversity (mean over all populations $H = 0.862$) and haplotypic richness (mean over all populations $A = 0.629$). These values are consistent with what is expected for *Cedrus* and for Mediterranean conifers in general (Fady, 2005; Fady *et al.*, 2008). The lowest diversity estimates were found in the Middle Atlas ($H = 0.854$ and $A = 0.573$). Differentiation among populations measured using an analysis of molecular variance (AMOVA) was low (2% among populations within regions and 1% among the three regions, see Table 1) but statistically significant ($P < 0.01$). Differentiation among regions became non-significant when only populations from High and Middle Atlas mountains were considered. Mean genetic distances (Nei, 1987) were computed and used in a neighbour-joining analysis (Saitou & Nei, 1987). The dendrogram (Fig. 5) was drawn with the program PHYLIP (Felsenstein, 2003). The results of this analysis demonstrate that there is a spatial genetic structure in current *C. atlantica* populations, although it is weak and not clearly related to the major geographic structures of Morocco. Similar results were obtained by Renau-Morata *et al.* (2005) using RAPD (random amplified polymorphic DNA) markers. The correlation between genetic and geographic distances using a Mantel test indicates isolation by distance among populations ($r^2 = 0.087$, $P = 0.03$). The correlation remained significant when only Rif and Middle Atlas populations were considered ($r^2 = 0.177$, $P = 0.03$), although it became non-significant when only Middle and High Atlas populations were considered. Put together, this evidence suggests that modern Moroccan cedar populations recolonized fairly recently (low differentiation) from one main refugial zone (significant isolation by distance), potentially the High Atlas, where the within-population diversity estimates are the highest. The

Table 2 List of Moroccan populations of *Cedrus atlantica* sampled for the genetic analysis.

Population	Code	Region	Latitude N	Longitude W	Elevation (m a.s.l.)	Precipitation (mm year ⁻¹)	Sample size
Idikel	IDIK	High Atlas	32°29	5°28	1950	450	20
Tounfite	TOUN	High Atlas	32°17/32°25	5°20/5°25	2050	450	21
Assaka	ASSA	High Atlas	32°23	5°23	2050	450	21
Tazekka	TAZE	Middle Atlas	34°08	4°10	1700/2000	1350	21
Tamtroucht	TARO	Middle Atlas	33°48	4°02	1800	750	21
Taffert	TAFF	Middle Atlas	33°38	4°10/4°06	1950	750	20
Seheb	SEHE	Middle Atlas	33°21	5°14	1700/1800	1100	22
Sidi M'guild	MGUI	Middle Atlas	33°25/33°15	5°14	2100	900	20
Ijdrane	IJDR	Middle Atlas	33°07/33°11	5°24/5°19	1700	900	20
Bou-Cedre	BOUC	Middle Atlas	32°50	5°23	1650	900	20
Tatgaline	TAGA	Middle Atlas	33°04	5°07	1800	1000	21
Col Du Zad	CZAD	Middle Atlas	33°02	5°05	1950		20
Talarine	TARI	Middle Atlas	32°53	5°12	1900	1000	21
Jbel Kelti	KELT	Rif	35°22	5°21	1700	1750	20
Tizi Ifri	IFRI	Rif	34°52	4°16	1850	1350	20

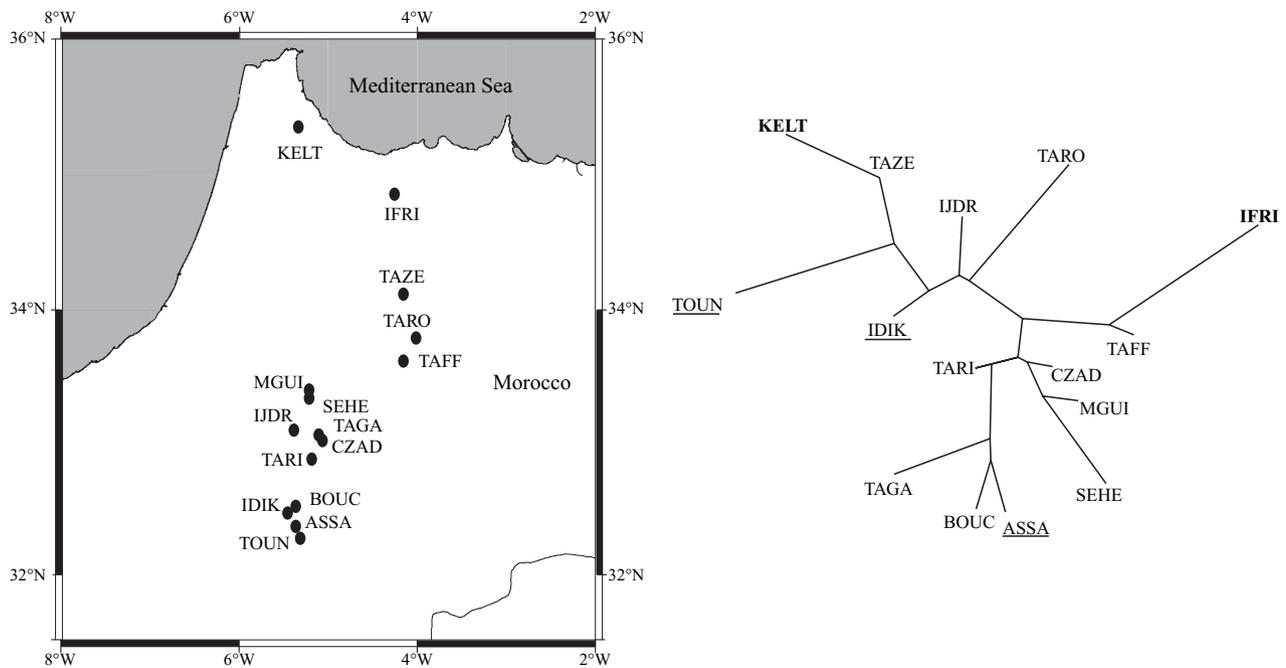


Figure 5 Locations of the cedar populations sampled for genetic study (details provided in Table 2) and a phylogenetic tree (neighbour-joining method) of Moroccan cedar. *Cedrus atlantica* populations from the Rif mountains are in bold type. Those from the High Atlas are underlined. All other populations are from the Middle Atlas. Site codes as in Table 2.

presence of a second refugial zone, centred on the Rif, is also possible. This area contributed significantly to the observed differentiation. It had a higher than average genetic diversity and contained 25% of the detected private haplotypes. The confirmation of independent refugia in the Rif and High Atlas requires a population sample larger than that currently available.

MODELLING THE POTENTIAL DISTRIBUTION OF *CEDRUS ATLANTICA*

Two main types of vegetation models are available for predicting species distributions (Kearney, 2006): static equilibrium models, which predict the probability of occurrence of a species (Jiménez-Valverde *et al.*, 2008), and dynamic global vegetation models (DGVM), which integrate processes of plant growth, competition, mortality and changes in ecosystem structure (Cramer *et al.*, 2001).

We used the DGVM CARAIB (CARbon Assimilation In the Biosphere) to simulate the modern and the year 2100 geographical distributions of *C. atlantica*. CARAIB is a mechanistic model that simulates the carbon cycle in the terrestrial biosphere (Hubert *et al.*, 1998; Otto *et al.*, 2002). It simulates the carbon stored in vegetation and the flow of carbon between vegetation, air and soil (Warnant *et al.*, 1994; Hubert *et al.*, 1998; Warnant, 1999; Otto *et al.*, 2002; Laurent *et al.*, 2004). Its spatial resolution is $10' \times 10'$ longitude and latitude. The computation step is 1 day for the updating of reservoirs. The flows of photosynthesis and autotrophic respiration are assessed every 2 h to accommodate the variation of solar

radiation and temperature during the day. One of the most important outputs of the model is the net primary productivity (NPP), which corresponds to the net absorption of carbon by plants.

CARAIB simulates potential, rather than actual, geographical distributions, which correspond to areas where climatic conditions theoretically allow the occurrence of the plant species. Actual areas never correspond to all potential ones as there are factors other than those integrated by the model (such as human disturbance) involved in the distribution of the species. As suggested by Svenning & Skov (2007a,b), historical issues such as rates of post-glacial dispersal may represent a limitation to simulating properly the modern geographical distribution of a tree species.

CARAIB requires a number of climatic variables as input. These are the mean daily temperature in $^{\circ}\text{C}$, the amplitude of the diurnal variation of temperature in $^{\circ}\text{C}$, the relative sunshine in %, the relative humidity of the air in %, the horizontal wind speed in m s^{-1} , and the precipitation in mm. The climatic data in the study area were provided monthly (12 climatological values) on each grid-cell space. The soil texture is also one of the inputs to the model. It allows an assessment of the conductivity of soil water used in the calculation of flow, runoff and drainage. In addition, each plant type is characterized by a set of parameters describing its climate tolerance.

For simulating the present day (Fig. 1b), we used a $10' \times 10'$ climate data set (New *et al.*, 2002). The climate variables were interpolated from data from weather stations for the period 1961–90. The climate data set for the year 2100 corresponds to the difference between the present-day climatology and the one

simulated by the ARPEGE model following the A2 scenario of the IPCC (2007).

The simulation reference was the atmospheric concentration of CO₂ in 2000 of 368 ppmv (IPCC, 2007). Obviously, the concentration of atmospheric CO₂ has an impact on plant growth and hence on biomass. The variable output from the CARAIB model representing growth is the NPP. Significant NPP values (*c.* 400–800 g C m⁻² year⁻¹) were simulated in the Atlas and the Rif. *Cedrus atlantica* was well simulated over all its modern distribution (Fig. 1b). The Rif and the Middle Atlas showed the highest NPP values (550–600 g C m⁻² year⁻¹). They were lower (0–350 g C m⁻² year⁻¹) in the Algerian mountains, where *Cedrus* occurs. These values were slightly lower than those simulated for the western part of the High Atlas, where cedar is absent. The simulated absence of cedar in Tunisia is coherent with its modern geographical distribution. As observed in the climate reconstructions above, January temperatures increased strongly following the last glacial period, and the low elevations in Tunisia did not allow cedar to compensate for that warming by migrating to higher altitudes. Winter temperatures higher than +5°C may substantially reduce cedar germination (Takos & Merou, 2001). Thus, the present absence of cedar from Tunisia is very probably related to winter warming during the Holocene rather than to anthropogenic pressure. Our simulations also show that some areas in Spain, such as the southern slopes of the Baetic massif, could be suitable today for *C. atlantica* (Fig. 1b). A fossil pollen record from Padul (Pons & Reille, 1988) showed that *Cedrus* was not present during the last glacial period. Thus, its absence today from mountainous areas of southern Spain could be related either to the lack of any glacial refugia in the area and/or to the fact that it did not spread from its northern African refugia.

For the simulation for the year 2100, the concentration of CO₂ in the atmosphere was taken to be 750 ppmv. This concentration (scenario A2 of the IPCC, 2007) is twice as high as that in the year 2000. In this simulation, considerable changes in the potential geographical distribution of cedar are observed. Its presence in North Africa is greatly threatened, as it is restricted to a few isolated patches in Morocco. According to our simulations, the western part of the High Atlas could be its only viable future refugium.

DISCUSSION

In northern Africa, unlike in Europe, Quaternary climate change and its impact on species geographical distributions is very poorly documented. *Cedrus atlantica* is a major species in Mediterranean ecosystems, especially in northern Africa, where seeds and seedlings have been collected by foresters and planted with success in the northern borderlands. The geographical distribution of *C. atlantica* has changed tremendously during the late Quaternary in northern Africa. Pollen data (Fig. 2) indicate that cedar was present during the last glacial and the post-glacial period in Algeria (Salamani, 1993), Tunisia (Ben Tiba & Reille, 1982) and Morocco (this study). In the Chataigneraie and Dar Fatma sites, cedar became extinct

during the Holocene, after *c.* 8 ka (Fig. 2), whereas it persisted in the Middle Atlas, Morocco. Both genetic data and fossil pollen analyses indicate that the *C. atlantica* in Morocco originated from a few local glacial refugia, possibly just one (or two) located in the High Atlas (and Rif). Hence, during the Pleistocene, cedar forests were able to migrate following climatic change in much the same way as major forest species did in Europe (Svenning & Skov, 2007b).

Temperatures in the Last Glacial Maximum (LGM) were *c.* 15°C colder than now, with an average annual precipitation around 300 mm. Like our climate reconstructions, several studies have shown that arid conditions prevailed over northern Africa during the LGM (Street & Grove, 1979; Gasse & Fontes, 1992). These arid conditions, which have probably affected most of northern Africa, restricted *C. atlantica* to several isolated refugia, including areas around Lake Ifrah in Morocco, Chataigneraie in Algeria and Dar Fatma in Tunisia. At the end of the last glacial period, a noticeable and abrupt warming took place. Like the Lake Tigalmamine pollen record (Cheddadi *et al.*, 1998), the reconstructed January temperatures for Chataigneraie and Lake Ifrah (Fig. 4) confirm that the early Holocene was warmer than today by *c.* 2–3°C. According to Salamani (1993), cedar migrated to higher altitudes towards the Djurdjura mountains, Algeria. Thus, the warming at the beginning of the Holocene probably forced cedar to migrate to higher altitudes. As a result, it gradually disappeared from Chataigneraie in Algeria and from Dar Fatma 1 in Tunisia, where the altitudes are lower than 1250 m a.s.l.

The expected increase in January temperature of more than 3°C during this century will lead to a January temperature even higher than that in the early Holocene, when *Cedrus* migrated to higher elevations or disappeared. Simulated vegetation distributions have shown that the geographical distribution of the whole thermo- and meso-Mediterranean ecosystem will be substantially affected during the next century (Cheddadi *et al.*, 2001). The simulations we performed for the year 2100 confirm these dramatic changes, revealing a significant reduction of the potential distribution of *C. atlantica* in North Africa (Fig. 1c). The climate change is expected to occur over less than a century, which might not give cedar forests enough time to adapt or to migrate. Only a few very restricted areas located in the High Atlas are predicted to be favourable for the survival of *C. atlantica*. It will disappear from the Rif mountains, the central part of the High Atlas, the middle Atlas and the northern mountains of Algeria. The south-western part of the High Atlas, from which *Cedrus* is now absent, seems to be the most suitable future refugium. We suggest that translocating populations of *C. atlantica* into areas simulated as future refugia represents a viable option, and that seeds or seedlings should be collected in the High Atlas mountains, where the highest genetic diversity has been found.

CONCLUSIONS

To summarize, the genetic data indicate that *C. atlantica* populations in the Rif have the highest genetic diversity.

Palaeodata suggest that cedar can migrate to higher altitudes and become locally extinct at lower altitudes in response to climate warming, but that future climate warming may be too rapid for it to migrate. Our model simulations show that the expected future climate change will reduce the geographical distribution of cedar and that a potential survival area is located in the south-western part of the High Atlas. On the basis of these findings, we suggest that one way to ensure the survival of *C. atlantica* would be to transplant seedlings from the High Atlas mountains to its south-western part.

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BIOSKETCH

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