## Abstract

1. **The greening of the Sahara, associated with the African Humid Period (AHP) between ca. 14,500 and 5,000 years ago, is arguably the largest climate-induced environmental change in the Holocene; it is usually explained by the strengthening and northward expansion of the African monsoon in response to orbital forcing. However, the strengthened monsoon in early to mid-Holocene climate model simulations cannot sustain vegetation in the Sahara or account for the increased humidity in the Mediterranean region.**
2. **In this article, we present an 18,500 year-long paleoclimate record from Lake Tislit in Morocco (32°N) that provides the first quantitative reconstruction of rainfall seasonality in northern Africa. The Tislit record shows that increased humidity in the AHP extended up to the North Saharan and Mediterranean regions due to increased winter rainfall, rather than summer monsoon rainfall.**
3. **Using a mechanistic vegetation model, we tested a hypothetical scenario at 9 ka of a progressive south-north gradient from summer to winter rainfall, rather than a precipitation increase over the monsoon season only. This scenario is based on increased winter rainfall in the northern Sahara that is related to reduced winter insolation and a southern shift of the winter storm track at 9 ka. These model simulations yielded a more realistic representation of the Green Sahara. This new conceptual framework should be taken into account in Earth System paleoclimate simulations used to explore the mechanisms of African climatic and environmental sensitivity.**
4. **Keywords:** African Humid Period, Green Sahara, Holocene, Paleoclimate reconstructions, vegetation model simulations

## Significance Statement

1. Explaining the greening of the Sahara during the Holocene has been a challenge for decades. A strengthening of the African monsoon caused by increased summer insolation is usually cited to explain why the Sahara was vegetated from 14,000 to 5,000 years ago. Here we provide a unique climate record of quantified rainfall seasonality in Morocco over the past 18,500 years and numeric simulations which show that moisture contributions from the Mediterranean Sea and the North Atlantic Ocean in winter were as important as the expanded summer monsoon for the greening of the Sahara during the African Humid Period. The findings of this study will help to better understand and simulate climate variability over northern Africa.

## Introduction

1. Moisture availability in northern Africa, from the Sahel to the Mediterranean coast, is a critical issue for both ecosystems and human societies and represents one of the largest uncertainties in future climate simulations1,2. During the early to mid-Holocene, northern Africa was wetter than today3-13, which allowed semi-arid, sub-tropical and tropical plant species to spread outside their modern ranges14 and human populations to inhabit a greener Sahara5,15. The humid time span in the African Sahel and Sahara, known as the African Humid Period (AHP), occurred in northern Africa after the last glacial period4,10,11,14,16,17 and lasted from ca. 14.5 ka (thousand years ago) to ca. 5 ka, with an optimum between 11 and 6 ka11,17.
2. The Green Sahara is an example of extreme environmental change, which highlights the region’s extraordinary sensitivity and the need to better understand its hydroclimatic variability. Current explanations for the greening of the Sahara point to the Earth's orbital changes during the early Holocene, leading to increased boreal summer insolation, which drove the intensification and northward expansion of the summer monsoon over northern Africa16,18. Reproducing the Green Sahara has posed a lasting challenge for climate modelers. The influence of the African monsoon does not extend further north than ~24°N in mid-Holocene simulations (with or without interactive vegetation), which is not sufficient to maintain a vegetated Sahara, and does not align with paleoclimatic evidence showing substantially increased humidity up to at least 31°N11,13. Models integrating vegetation and dust feedback provide improved simulations but still produce discrepancies with proxy data18,19,21. Additional sources of moisture22,23 may have contributed to an AHP that extended toward the Mediterranean borderlands through different mechanisms. However, identifying the moisture sources over North Africa during the AHP requires paleoclimate records of precipitation seasonality.
3. In the High Atlas Mountains, we collected an 8.5 m long sediment core from Lake Tislit (ca. 32°N): an endorheic lake that is sensitive to hydroclimatic changes and acts as a trap for pollen grains from the surrounding landscape. It is ideally located for capturing the climatic variability of the Mediterranean and northwestern Sahara (figure 1). The Tislit sequence yielded unique hydrological data from leaf-wax stable isotopes and ostracod δ18O, as well as a quantified time series of seasonal rainfall from the fossil pollen assemblages. Based on the seasonal precipitation reconstructed from the Tislit record, hypothetical AHP rainfall regimes in northern Africa were then tested by feeding them into a dynamic vegetation model, and comparing the simulated vegetation to the observed Green Sahara vegetation.

## Results and Discussion

1. From the Tislit sediment core, we obtained a continuous, radiocarbon-dated record of the last 18,500 years (figure S1). Its pollen content (figure S2) shows a general predominance of Mediterranean ecosystems, with arid steppe elements (*Artemisia* and Chenopodiaceae), between 18.5 ka and 15 ka, and sclerophyllous evergreen tree and shrub taxa (*Pinus, Quercus, Olea, Pistacia*) during the AHP. After 5 ka, the landscape continued to be dominated by pine and oak trees, with recolonization by the steppic sagebrush. Mediterranean plant species such as *Olea* and *Quercus* evergreen are physiologically adapted to summer drought24-26 and grow according to a marked seasonal distribution of precipitation over the year (figure S3). The spread of these and other Mediterranean plant taxa to Tislit during the Holocene (figure S2) clearly indicates higher precipitation in winter than in summer. For the first time, the Tislit pollen record allowed us to quantitatively reconstruct the seasonal changes of temperature (figure S4) and precipitation (figure 2) in northern Africa, using the overlapping climatic ranges of pollen taxa (see methods). These climatic ranges were obtained from an extensive database of georeferenced modern plant distributions. The accuracy of the method was validated for Morocco by comparing precipitation reconstructed from an extensive modern pollen dataset to instrumental values (figure S5, see methods).
2. The pollen-based reconstruction shows that summer rainfall (figure 2h) has not changed significantly over the past 18,500 years while winter (figure 2f) and spring (figure 2g) rainfall increased by ~30 % between ca. 14 ka and ca. 9.5 ka, reaching their highest values between ca. 10.5 and 8.5 ka, which corresponds to the AHP, as evidenced in northern African sites10, then decreased by ~15 % by ca. 5.7 ka. This result, obtained using a mathematical technique, quantifies the inference based on the ecological and physiological requirements of the fossil plant taxa. The increase in annual precipitation during the AHP (figure 2e) is thus robustly related to a higher contribution from winter and spring rainfall, rather than to summer rainfall, which remained almost unchanged through the whole period (figure 2h). Temperature has an impact on water availability for plants through evaporation, which may affect the composition of the ecosystems. However, rainfall in the Mediterranean area occurs during the cold season, when temperature has a minor evaporation effect on the total water budget. In the case of Tislit, the reconstructed mean January temperature (figure S4) varied by about 2 °C during the Holocene (between 2 °C and 4 °C), which had a negligible effect on water availability. Summer temperature also had only a minor effect, since Mediterranean species are adapted to long periods of drought.
3. Stable oxygen isotopes (18O) of ostracod shells from the Tislit core were also analyzed (see methods). Given that Lake Tislit has no outlet, the 18O record (figure 2a), corrected for temperature changes, reflects variations in the lake’s hydrological budget. Highly depleted 18O values observed between 18 ka and 13 ka indicate a massive increase in freshwater input, resulting from the melting of a glacier that stood close to the lake27. After the disappearance of the glacier at ca. 12 ka27, 18O variations reflect changes in the precipitation-evaporation budget and suggest humid conditions in the early Holocene, followed by a progressive aridification that is consistent with the pollen record.
4. Leaf-wax stable hydrogen isotope (D) compositions were measured (see methods, figure S6) to assess precipitation isotope changes (figure 2b) during the plant growing season28. Given that it is more directly linked to precipitation and not as influenced by evaporation, there are substantial differences between the leaf wax D record and the ostracod 18O record. However, the former does clearly record a period with isotopically depleted precipitation that is consistent with increased rainfall between 11 and 5 ka.
5. Although pollen-derived precipitation and Dprecip estimates are broadly in phase in the Tislit record, some significant differences indicate that Dprecip estimates are not solely driven by the effect of precipitation. Morocco currently has three main moisture sources: the northern Atlantic Ocean, the central Atlantic Ocean and the Mediterranean Sea29. The northern Atlantic moisture source provides the most isotopically depleted rainfall, followed by the central Atlantic, and then the Mediterranean source, which is the most isotopically enriched29. Therefore, it is likely that the depleted Dprecip estimates during the AHP (figure 2b) indicate a predominance of remote, northern Atlantic moisture. The abrupt enrichment in Dprecip estimates at 5 ka, which is not reflected in the pollen-based precipitation estimates, was therefore likely related to the sudden cooling in the North Atlantic Ocean caused by a reduction in the Atlantic thermohaline circulation at that time30. This would have decreased the importance of the remote northern Atlantic (the isotopically depleted moisture source) in favor of the relative contributions of the proximal central Atlantic and the Mediterranean (isotopically enriched moisture sources). In summary, the Dprecip estimates at Tislit record the amount of precipitation, overprinted by moisture-source effects.
6. **Sources of AHP moisture in the northern Sahara**
7. An analysis of precipitation variability over the 1901-2010 period in Morocco shows that the amount of winter precipitation in Tislit is strongly and significantly correlated with a wider adjacent area (figure 1C). This allows us to surmise that the Tislit paleoclimate record is not a local feature, but representative of the climate history of a larger region that includes at least northwestern Sahara and the Mediterranean region. In addition, there is a strong coherence between the Dprecip record from Lake Tislit (figure 2b) and the Dprecip record of marine core GC27 (figure 2c) from offshore Morocco11 (figure 1), with regards to the timing of the two depleted peaks at 15 - 12.7ka and 11 - 5ka, which are separated by a relatively drier episode during the Younger Dryas. This double peak signal is also observed further south in the Sahel and in Equatorial Africa10,11,31. Considering the proximity of core GC27 – located at about the same latitude but ~450 km away from Lake Tislit – the similarity of their leaf wax D records, and the fact that Tislit precipitation variability is now strongly correlated with that in the catchment that contributed sediments to core GC27 (figure 1C), both sites most likely recorded a similar climate regime. Consequently, the increased precipitation recorded during the AHP in the GC27 marine core, and possibly in the CG37 core located at 27°N11, was not associated with the African summer monsoon but rather with winter and spring rainfall, as for Lake Tislit. In both climate systems, the similarity of the Dprecip records was probably caused by an increase in precipitation in parallel with the prevalence of a remote moisture source (northern Atlantic Ocean versus Gulf of Guinea), meaning that Dprecip is not indicative of specific moisture sources (summer monsoon versus winter storm tracks).
8. Numeric simulations of the Earth’s climate forced by precession changes have shown that during periods of maximum boreal summer insolation and minimum boreal winter insolation, such as the early Holocene, the equator-to-pole temperature gradient is decreased in winter, which is associated with a southern shift of the Hadley cell, the westerlies, and the Mediterranean storm track, bringing increased winter precipitation to northern Africa23. Although simulations show this mechanism to have a relatively small rainfall effect in northern Africa, it is qualitatively consistent with our observations. The in-phase variability of Mediterranean winter rainfall with the North African summer monsoon during precessional cycles has also been identified in paleoclimate records from the northern Mediterranean32. We suggest that the strengthened Mediterranean winter storm track reached northern Africa as a response to lower winter insolation, and may have been the moisture source for the increased winter rainfall in the northern Sahara during the Holocene AHP.

## An alternative precipitation model to explain the Green Sahara

1. Today, the African monsoon reaches ~15°N33, while the Mediterranean winter rainfall zone is limited to a narrow band close to the Mediterranean coast (figure 1). These two rainfall zones are separated by a vast desert that receives less than 100 mm rain per year34. We propose that the Mediterranean rainfall zone and the African monsoon zone expanded south and north, respectively, and overlapped during the AHP, thereby sustaining a Green Sahara. Fossil pollen data indicate that the Green Sahara was composed of Sahelian biomes south of 24°N and a steppe biome in the north3. Middle and early Holocene simulations suggest that the African monsoon may have reached 24°N, depending on model and experimental settings, if we exclude sensitivity experiments that prescribed extended vegetation20. In the LOVECLIM Earth system model, orbitally paced humid periods such as the early Holocene are associated with intensified westerlies in northern Africa and the occurrence of low pressure anomalies as far south as 18°N32. We therefore propose that the influence of the winter storm track shifted south during the AHP to reach at least 24°N, and potentially 18°N.
2. This means that an environment characterized by two rainfall seasons would have existed during the AHP between 18°N and 24°N. The total annual precipitation in this zone was probably small, given its location at the boundary of both precipitation systems. However, even with low rainfall levels, two wet seasons would have had a major impact on ecosystems, because their primary effect would have been the reduction of the dry season (less than 50 mm of rainfall/month) to under 6 months, instead of 10-11 months if rainfall had only been brought by the summer monsoon. The length of the dry season in arid regions has a direct impact on ecosystems35,36. A reduction of the dry season through a distribution of the total annual rainfall over both winter and summer would sustain vegetation better than a larger amount of rainfall occurring in a single season. This would also be expected to affect the Saharan albedo and its feedback on climate.

## Testing Green Sahara precipitation regimes with a vegetation model

1. We tested this paleoclimate hypothesis by simulating its impact on the Sahara with the CARAIB dynamic vegetation model (see methods), whose performance is well-tested37-40. Biomes and net primary productivity, simulated in a control simulation forced with modern climate data, correctly reproduce the vegetation observed today in northern Africa (figure S7). Three different precipitation regimes were tested as inputs into the vegetation model under 9 ka insolation and atmospheric CO2 conditions (figure 3). In simulation A, CARAIB was forced by the rainfall regime produced by the HadCM3 model paleoclimate simulation at 9 ka, and corrected for its modern biases41 (A1). Simulation A is an illustrative example of climate model simulations of the early Holocene. Simulations B and C are idealized scenarios to test the effect of rainfall seasonal distribution on Sahara biomes and net primary productivity (NPP) at 9 ka, where 300 mm.year-1 was added to the modern precipitation regime over the whole of northern Africa, with two different seasonal distributions. The rainfall increase of 300 mm.year-1 lies within the range of quantitative estimates derived from fossil pollen records in the Green Sahara42,43. The additional annual precipitation was distributed in the summer season (JJA) in simulation B as a simplified representation of the hypothesis that the AHP was related solely to a strengthened African monsoon (B1). Simulation C is a test of the alternative model proposed, in which the additional 300 mm.year-1 was seasonally distributed from north to south to represent a gradual winter rainfall penetration down to 18°N, combined with a gradual northward expansion of the summer monsoon up to 24°N, thus including an overlap zone with a weak double rainy season between 18°N and 24°N (C1).
2. The first simulation (A) yielded vast semi-desert or desert biomes (A2) across the whole Saharan belt, with an NPP under 50 g.C.m-2.yr-1 (A3). The precipitation regime produced by the HadCM3 model at 9 ka fails to sustain a Green Sahara, in line with most climate system models44. Simulations B and C both show higher NPP as expected, but with striking differences that confirm the strong effect of rainfall seasonality on vegetation in the Saharan belt.
3. In the monsoon-only scenario (B), the Sahara is still largely dominated by a semi-desert biome (B2), with NPP values below 50 g.C.m-2.yr-1 (B3), despite the additional 300 mm of rainfall. This is neither compatible with the vegetation reconstructed at 6 ka in Lake Yoa6, nor with evidence of pastoralism across the Sahara in the early Holocene5. In addition, subtropical biomes appear close to the Mediterranean coast in Morocco, which is also in contradiction with our pollen record and others from a lower elevation in the Atlas mountains45,46. In contrast, with the same annual rainfall, the sensitivity test combining Mediterranean winter rainfall and summer monsoon rainfall (C1) yields higher NPP values (C2) and biomes (C3) that are consistent with observations14. In this simulation, the semi-desert is reduced to patches and several vegetation corridors that were necessary for plant species migration14 are present. Simulation C is in agreement with observed data both in the input and output, which indicates theoretical progress in this experiment.
   1. The realistic Green Sahara produced by vegetation simulation C, in contrast to B, provides evidence of a more complex climate response to early Holocene insolation forcing, combining a strengthening and southward shift of the Mediterranean winter rainfall zone into the northern Sahara with a northward expansion of the summer monsoon belt. Increased winter rainfall over the northern Sahara was necessary in order for the Green Sahara to persist over a time span of several millennia.

## Conclusions

* 1. In this study, we presented a paleoclimate record of seasonal precipitation from Lake Tislit in Morocco (32°N), which provides the first objective observational constraint on the northward expansion of the African monsoon that is usually cited to explain the AHP in northern Africa between 14.5 ka and 5 ka. Isotopic and pollen evidence confirm that Morocco was wetter than today during the AHP, as was the rest of northern Africa, but that the increase in humidity was related to winter rainfall rather than summer monsoon rainfall at this latitude. This constraint brings about a new paleoclimate scenario for the AHP and the Green Sahara. Using a dynamic vegetation model, we have shown that the Green Sahara is best represented under 9 ka conditions with Mediterranean winter precipitation penetrating southward down to 18°N, while the summer monsoon is shifted northward and strengthened up to 24°N. Additional climate records of seasonal precipitation levels during the African Humid Period are needed, especially between 18°N and 24°N, to track the latitudinal position of these rainfall systems. The climatic process linking the early Holocene insolation to the increased winter precipitation in northern Sahara also needs to be explored. This new conceptual framework represents an important shift in the target for evaluations of IPCC Earth system models and their ability to simulate African climate variability47,48.

## Materials and methods

### The geographical setting of the Tislit record

1. Morocco is located in Northwest Africa and has vast coastal areas, a mountainous interior (the Atlas Mountains) and large deserted regions that extend south. The climate is Mediterranean, with winter moisture transported via storm tracks from the Atlantic Ocean and the Mediterranean Sea, and a dry summer season dominated by Saharan air masses. In the High Atlas Mountains, we collected an 8.5-meter-long sediment core (32°11'N 5°38'W, 2250 m asl) in 2016, under a 5 m water column in the NE part of Lake Tislit, using a Russian corer.
2. Lake Tislit extends about 1.2 km E-W and 600 m N-S in a tectonic pull-apart basin that was formed within Jurassic red beds49 located south of the highest elevations of the central High Atlas. Today, the lake is mainly fed by snow melt during spring. Evaporation is high during summer, which leads to a lake-level change of several meters over the course of the year, but the annual precipitation to evaporation budget is still positive and the lake is permanent. The hills surrounding the lake are treeless except for few stands of pines (*Pinus halepensis*) and poplars (*Populus alba*) on the edge of the lake. The dominant vegetation is grasses. The local human impact on vegetation is minor because of the very low number of inhabitants at the elevation of the lake.
3. The chronology of the Tislit core is based on eight radiocarbon dates (figure S1). The 14C age calibration and the age-depth model were obtained with CLAM software version 2.250, using the calibration data set IntCal1351. The age-depth model provides a basal age of about 18,500 years cal BP. The accumulation is continuous and rather constant in the whole core. We collected 171 samples from the Tislit core in 5 cm intervals, which corresponds to an average time resolution of about 100 years. The samples were then sub-sampled for pollen and ostracods, and subjected to stable oxygen isotope analyses and leaf wax analyses.

### Pollen analyses

1. A set of 171 sub-samples were treated chemically to extract their pollen content, using HCl, KOH, ZnCl2 and acetolysis (sulfuric acid and acetic anhydride). Pollen grains were identified and counted using a photonic microscope. We identified 78 pollen taxa, of which 10 were aquatic. The pollen sums and percentages in each sample are based on trees, shrubs and herbs, and exclude aquatic plants and fern spores. The number of pollen grains counted per sample was between 108 and 758 (with a mean of ca. 220). Ten samples were pollen barren, 7 of which were in the uppermost section (0 to 35 cm). Thus, the uppermost pollen sample is dated at ca. 1000 years BP.

### Pollen-based climate reconstruction

1. Fossil pollen data from temperate ecosystems with a markedly seasonal climate, such as the Mediterranean, are a powerful climate proxy for evaluating past seasonal changes in precipitation. As an illustration from the Tislit pollen data, herbs or trees such as *Asphodelus* or *Olea* require low levels of precipitation during summer (less than 50 mm in JJA) but require more than 300 mm in winter (DJF) (figures S3 and S8). Their co-occurrence in the pollen record allow these seasonal precipitation levels to be reconstructed. Conversely, the co-occurrence of taxa such as *Ilex aquifolium* and *Salix*, for instance, would reflect a smaller seasonal contrast (figure S8). In the rest of this section, we describe the quantitative reconstruction process and its uncertainties.
2. The first step was the assignment of fossil pollen taxa to modern plant species. Pollen grains are often identified to the family or genera level, because most species of the same genus produce pollen grains that are morphologically indistinguishable. Drawing on our background in palynology, botany and ecology, we assigned 45 of the pollen taxa identified in the Tislit record (table S1) to plant species that are available in a personal database, containing 864 geo-referenced distributions obtained from Flora Europaea52-54 and GBIF55. The remaining fossil pollen taxa (33) could not be included in the climate reconstruction because they were either aquatic, human-related, contained less than 1 % of pollen, or their georeferenced modern range was not available. The geographical occurrence of plants was crossed with modern interpolated climatology from the WORLDCLIM database56 to estimate the seasonal temperature and precipitation ranges of the fossil taxa.
3. The second step consisted of computing the median monthly precipitation values for the assigned plant species based on their modern climate ranges (figure S8). The changing contributions of species within a pollen taxon does not affect the reconstruction, since the pollen taxon’s climatic envelope always includes the species envelope.
4. The fossil pollen samples contain different numbers of taxa and distinct taxa, meaning that the median precipitation values vary from one sample to another. The reconstructed monthly precipitation value corresponds to the weighted median (pollen percentages were used as weights) of the medians of the climatic ranges corresponding to those taxa identified in a fossil sample. The reconstruction uncertainty is estimated using a jackknife procedure, leaving a taxon out at each iterative climate estimation, as many times as the number of taxa in each fossil sample.
5. In contrast to other pollen-based climate transfer function techniques, our method is not affected by the fact that past plant communities (and fossil pollen assemblages) may not exist today, because pollen taxa may only co-occur if the source plant species co-existed and there was therefore an overlap of all their climatic variables. This hypothesis regarding the overlap of species’ climatic ranges is valid for both modern and past ecosystems and takes into account a potential range shift in the species’ realized niche57.
6. The small variation in atmospheric CO2 during the Holocene (roughly between 250-270 ppmv)58 had less impact on the ecosystems than during the LGM59, and should therefore represent a negligible bias in the reconstructed precipitation values during the AHP.
7. Pollen grains are mainly dispersed by wind (pollen grains from entomophilous plant species are rather rare in the fossil samples), meaning that some may be transported over long distances and affect the estimated climate. These pollen grains usually do not exceed 1 % of the total pollen sum, which is the threshold we used to select pollen taxa and avoid this error source in the climate reconstruction.
8. We tested the pollen-based climate reconstruction method with a modern dataset of pollen samples collected in Morocco60 (figure S5). The estimated climate values were compared to the WORLDCLIM dataset56. The reconstructed annual, winter and spring values correlated rather well (r>0.6) with the observed climate. Summer reconstructed and observed precipitation correlated less well (r=0.43), due to the low amounts of rainfall and their more stochastic occurrence. Precipitation is generally overestimated in arid areas because all plants are in the limit of their range, while the method considers species’ optimum climate value to be the most likely estimate. Thus, the pollen-based climate reconstruction approach should be used with caution in areas where annual precipitation is lower than ca. 300 mm.year-1. Tislit, however, lies in the climatic range that is not affected by this bias (figure S5). The spread of the reconstructed values in this test does not reflect the uncertainty of the method, because the modern pollen dataset stems from soil and moss samples that might be affected by their highly specific, heterogeneous environments, while Tislit is a sediment record from a large lake into which the vegetation changes of the surrounding landscape have been continuously integrated.
9. All statistics and database queries were performed using R software version 3.6.361 with Akima62, RMySQL63, and Stats libraries61.

### Oxygen isotopes from ostracod shells

1. Of the 171 samples collected from the Tislit core, 142 sub-samples of 1 cm3 sediment were disaggregated in de-ionized water with detergent, then rinsed, sieved, and dried. Ostracod shells were picked out, cleaned a second time by ultrasonication in methanol and dried. Dry ostracod remains (mostly disarticulated carapace valves and their larger fragments) were identified under a microscope at up to 500× magnification using taxonomy identification keys64.
2. When possible, 30 ostracod shells of the last four (5th-8th) juvenile stages (mostly 0.49 - 0.83 mm in length) of a species belonging to the genus *Candona* were picked out for isotopic analysis. This genus was selected for its abundance throughout the sediment core. By using the same taxon for isotopic analyses in the whole record, we avoided variations due to species-specific isotopic offsets65. Ostracod shells are composed of calcite. Scanning electronic microscope observations showed excellent preservation. Only 13 samples out of 142 did not have enough valves for isotopic analysis. The samples were dissolved in saturated phosphoric acid at 70 °C in a Kiel IV carbonate device. The oxygen isotopic composition of the CO2 obtained was measured in a Thermo Delta V mass spectrometer. The analytic reproducibility (±1σ) was 0.1 ‰ based on long-term analysis of standard laboratory calcite samples. Isotopic values (figure 2a) are reported in permil as deviations relative to the VPDB international standard. Ostracod isotopic values were corrected from the biological fractionation offset of +2.2 ‰ estimated for *Candoninae* Ostracods65. The lake water δ18O was estimated using the paleotemperature equation of Kim and O’Neil66 for inorganic calcite, and the pollen-derived annual temperature values (figure S4).

### Leaf wax analyses

1. For the leaf wax analyses we used 79 sub-samples from the Tislit core. Two to three grams of dried and finely ground sediment samples (n=89) were extracted in an ASE200 accelerated solvent extractor, using a dichloromethane (DCM):methanol (MeOH) 9:1 solution, at 1000 psi and 100 °C, for three cycles lasting 5 min each. Known amounts of squalane were added prior to extraction as an internal standard. The total lipid extracts (TLEs) were dried in a Heidolph ROTOVAP system. Residual water was removed over columns of Na2SO4, using hexane as an eluent. The TLEs were saponified in 0.5 ml of 0.1 M KOH in MeOH solution. After adding bi-distilled water, the neutral fractions were obtained by liquid-liquid extraction using hexane. The neutral fractions were separated over pipette columns of deactivated silica (1% H2O) using hexane, DCM and DCM:MeOH 1:1 as eluents to obtain apolar, ketone and polar fractions, respectively. The apolar fractions were further purified by cleaning them over columns of AgNO3-coated SiO2, using hexane as a solvent to remove unsaturated compounds. *N-*Alkanes were quantified using a Thermo Fisher Scientific Focus gas chromatograph (GC) equipped with a 30 m Rxi™-5ms column (30 m, 0.25 mm, 0.25 μm) and a flame ionization detector. Quantification was achieved by comparing the integrated peak areas to external standard solutions, consisting of *n*-alkanes of varying chain-lengths. Repeated analyses of standard solutions indicated a quantification precision of 10 %. All samples were dominated by odd-numbered long-chain *n*-alkanes, with *n*-C29 and *n*-C31 alkanes being the most abundant homologues in all samples. The CPI values67 of long-chain *n*-alkanes were 7.8 on average (3.6 - 15.4), indicating their origin in epicuticular waxes of terrestrial higher plants68.
2. 13C analyses of *n-*alkanes were conducted on a ThermoFisher Scientific MAT 252 isotope ratio mass spectrometer that was coupled, via a GC-C combustion interface with a nickel catalyzer operating at 1000 °C, to a ThermoFisher Scientific Trace GC equipped with a HP-5ms column (30 m, 0.25 mm, 0.25 μm). Each sample was measured in duplicate if sufficient material was available. δ13C values were calibrated against a CO2 reference gas of known isotopic composition, and are given in ‰ VPDB. Accuracy and precision were determined by measuring *n-*alkane standards, calibrated against the A4-Mix isotope standard (A. Schimmelmann, University of Indiana) every six measurements. The difference between the long-term means and the measured standard values yielded a 1σ error of <0.3 ‰. The accuracy and precision of the squalane internal standard were both 0.1 ‰. The precision of the replicate analyses of the *n*-C29 and *n*-C31 alkanes was 0.2 and 0.1 ‰ on average, respectively (<0.1 – 0.7 ‰ for *n*-C29 and <0.1 – 0.6 ‰ for *n*-C31 alkane). For samples which could only be analyzed once, the long-term precision of the standards (0.3 ‰) was assumed. As 13C values of the *n*-C29 and *n*-C31 alkanes co-vary strongly (r=0.81), we calculated a weighted average 13C value for 13Cwax using their relative abundance. 13Cwax varies from -33.3 to -24.5 ‰ VPDB, with an average propagated precision of 0.2 ‰ (<0.1 – 0.7). Mostly, 13Cwax showed depleted 13C values, indicative of C3 plant vegetation, with the exception of the period corresponding to Heinrich event 1 (HE1, 16.1 – 14.9 ka BP), during which there were enriched 13C values (figure S6). This is consistent with the natural vegetation in Morocco, which is entirely of the C3 type in modern conditions. The elevated 13Cwax values duringHE1 coincide with an abundance of Poaceae and could thus indicate an expansion of C4 grasses around Lake Tislit under the extreme climatic conditions of HE1.
3. D analyses of *n-*alkanes were conducted on a Thermo Fisher Scientific MAT 253™ Isotope Ratio Mass Spectrometer that was coupled, via a GC IsoLink operating at 1420°C, to a Thermo Fisher Scientific TRACE GC equipped with a HP-5ms column (30 m, 0.25 mm, 1 μm). Each sample was measured in duplicate if sufficient material was available. D values were calibrated against an H2 reference gas of known isotopic composition and are given in ‰ VSMOW. Accuracy and precision were controlled by the laboratory’s internal *n-*alkane standard, calibrated against the A4-Mix isotope standard every six measurements, and by daily determination of the H3+ factor. Measurement precision was determined by calculating the difference between the analyzed values of each standard measurement and the long-term mean of standard measurements, which yielded a 1σ error of <3 ‰. H3+ factors varied between 5.0 and 5.2. The accuracy and precision of the squalane internal standard were 4 ‰ and 3 ‰, respectively. The precision of the replicate analyses of the *n*-C29 and *n*-C31 alkanes was 1 ‰ on average (<1 – 5 ‰). For samples which could only be analyzed once, the long-term precision of the standards (3 ‰) was assumed. As D values of the *n*-C29 and *n*-C31 alkanes co-vary strongly (r=0.78), we calculated a weighted average D value for Dwax, using their relative abundance. Dwax varies between -162 to -193 ‰ VSMOW, with an average propagated precision of 2 ‰ (<1 – 5 ‰) (figure S6). As different vegetation types can cause offsets in Dwax, due to different hydrogen isotope fractionation factors, we estimated Dprecip using 13Cwax as an estimate for vegetation type, according to established procedures69. For comparability, we used 13Cwax endmembers and fractionation factors reported by Tierney11 and based on Garcin70 and Sachse71. Dprecip estimates range from -54 to -87 ‰ VSMOW (figure 5 in SI), which are consistently more depleted than the Dprecip estimates for GC2711. This is due to the high altitude setting of Lake Tislit and reflects the input of plant waxes from local sources. Additionally, the Dprecip estimates were compensated for global ice volume changes affecting isotopes in the hydrological cycle. For this purpose, Bintanja’s marine oxygen isotope compilation66 was used, with the LGM-present 18O range scaled to 1 ‰ VSMOW. This ice-volume correction has an insignificant effect for the Holocene and leads to slightly depleted Dprecip estimates for the period over 10,000 years ago (figure S6). In addition, we compensated the Dprecip estimates for temperature changes, as changes in condensation temperature lead to changes in Dprecip72. In the absence of a specific local temperature lapse rate for Morocco, we used the global average of 5.6 ‰/°C for Dprecip72. We used the averaged winter temperature (Dec - Feb) from the pollen reconstructions. The essential effect of the temperature compensation is more enriched Dprecip estimates when winter temperatures were lower, i.e. prior to the Holocene (figure S6).

### Vegetation model simulations

1. Vegetation was simulated with the CARAIB37-39 Dynamic Vegetation Model (DVM). This mechanistic model describes stomatal regulation and photosynthesis, growth and respiration, competition for resources, and mortality of a set of plant objects, which can be plant functional types (PFT), bioclimatic affinity groups or plant species. In this study, PFTs have been used in accordance with Henrot’s classification40, which includes 26 PFTs designed for large-scale or global applications. These PFTs are distributed between two vegetation stories: grasses and shrubs (PFTs 1-11) in the understory, and trees (PFTs 12-26) in the overstory. The model also calculates a budget of water fluxes to evaluate the amount of soil water in the root zone. Soil water deficit can induce: (1) stomatal closure and reduction of photosynthetic assimilation; (2) reduction of the leaf area index (leaf desiccation); and, under most severe water stress, (3) mortality of the PFTs. Natural fires can also induce mortality during dry periods. The model time step is 1 day for updating soil water or carbon reservoirs, and 2 hours for the calculation of photosynthesis and respiration fluxes.
2. The daily model inputs are mean air temperature T, diurnal thermal amplitude Tmax - Tmin, precipitation P, percentage of sunshine hours SH, air relative humidity RH, and wind speed W. The main model outputs are soil water amount and water fluxes, as well as the abundance, gross and net primary productivity (GPP, NPP), biomass and leaf area index of all PFTs. From these outputs, a biome map can be constructed in a post-processing subroutine37-39.
3. First, a control simulation was run at 280 ppmv of atmospheric CO2 (figure S7). The 1901-1930 period was used as a baseline, instead of the pre-industrial era, which lacks gridded climatological data. Climate data were taken from the Global Soil Wetness Project Phase 3 (GSWP3), as bias-corrected and distributed within the Inter-Sectoral Impact Model Intercomparison Project – Phase 2 (ISIMIP2a). This dataset covers the whole 20th century. It is based on the 20th-century reanalyses (prepared by the NOAA, see <https://www.psl.noaa.gov/data/20thC_Rean/>), and the meteorological data are provided with a daily time step. The GSWP3 data used in the 1901-1930 control climate provided a 30-year sequence of daily values for each of the model’s input climate variables. After a spin-up phase, the CARAIB model was run over this 30-year series and an average was calculated, before analyzing the results and plotting biomes and NPP maps.
4. In the first simulation (figure 3A), we selected the HadCM3 general circulation model41, as it performed an almost transient simulation over the last 21,000 years (with 1,000-year snapshots), with atmosphere and ocean grids of 3.75° x 2.5° and 1.25° x 1.25°, respectively, over 20 levels each. For the 9 ka experiments of HadCM3, only monthly mean data were available. The monthly anomalies were then calculated as the absolute anomaly (i.e., the difference between the 9 ka simulation and the pre-industrial control simulation) for temperature, and as a combination of the absolute and relative (i.e., the ratio between 9 ka and the control) anomaly for precipitation. This combination was chosen in such a way that it favored the absolute anomaly whenever possible, except when negative precipitation tended to be produced for 9 ka. In the latter situation, the weight of the relative anomaly was progressively increased73. The monthly anomalies were then simply added to the 1901-1930 monthly mean values, yielding a 30-year sequence of monthly temperature and precipitation for 9 ka. CARAIB’s weather generator was then used to produce the daily values necessary to force the simulations for each year, drawing on the monthly sequence. This weather generator is based on the currently observed day-to-day variability of temperature (minimum and maximum) and precipitation per (geo-)climatic zone. A renormalization process is performed to ensure that the monthly values are not altered74. Note that the day-to-day variability reconstructed by the generator differs from that of the GSWP3 1901-1930 signal. However, this should not significantly impact the results, since both variabilities are based on meteorological data collected in a similar climatic zone (hence with similar distribution functions), and a relatively long record (30 years) is generated.
5. In the first simulation (3A), the climatic anomalies between 9 ka and 0 ka from HadCM3 were computed, interpolated and added to the 1901-1930 climate series, to obtain a 30-year climate series for 9 ka at 0.5° x 0.5°. CARAIB was run, using this climate series as an input (repeated several times to relax the initial conditions) together with an atmospheric CO2 of 263 ppmv, both of which were characteristic of the early Holocene58. To calculate the solar flux in CARAIB, 9 ka orbital parameters were used, together with the percentage of sunshine hours.
   1. In the two sensitivity tests (3B and 3C), two 30-year climate series were constructed for 9 ka, by adding 300 mm of precipitation to the 1901-1930 series each year, uniformly over the whole simulated area. In the first case (B), the 300 mm was distributed in the summer months only (June to September), to simulate a strong northward shift of the monsoon up to the Mediterranean area (B1). In the second case (C), the 300 mm was mostly distributed at latitudes lower than 18°N in the summer months, and mostly at latitudes higher than 24°N in the winter months (November to February), and between 18°N and 24°N in both summer and winter (transition zone) (C1, table S2). CARAIB was run with these two 30-year series of climatic data in a 9 ka configuration (263 ppmv of CO2 and 9 ka orbital parameters).
6. For consistency, in simulations B and C, the air relative humidity r was increased and the percentage of sunshine hours s was decreased at the same time as the precipitation was increased. These changes in r and s are critical for maintaining a Green Sahara, since they significantly reduce evapotranspiration and thus lead to wetter soils. They were estimated on the basis of statistical relationships established in the simulated areas for the 1901-1930 period in our climate dataset.
7. Using the monthly climatological means for 1901-1930, a significant linear correlation was indeed obtained in a log-log plot of relative humidity r (or sunshine hours s) versus precipitation that was increased by 1 mm/month (P+1). The Pearson correlation coefficient was 0.772 for r and -0.759 for s, when all months and all pixels of the simulated domain were included. This yielded the following relationships, allowing us to calculate r and s as a function of precipitation P:
8. (5 < r < 100)
9. (0 < s < 100)
10. where r and s are expressed in % and limited to the indicated ranges, precipitation P is in mm/month, and αr = 23,0233, βr = 0,2153, αs = 88,8467, βs = - 0,0936193. These relationships allowed us to calculate the anomalies:
    1. to be added to each value of r and s in the 1901-1930 time series, to obtain a 30-year time series of r and s for simulations B and C.

### References

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### Authors’ contributions

1. RC designed the study, performed the pollen-based climate reconstructions, produced the figures and wrote the initial manuscript. MNEB analyzed the pollen content. MNEB and ES processed the leaf wax samples and conducted compound-specific isotope analyses. MC performed the oxygen isotope analyses. LF and RC designed the vegetation model sensitivity tests and LF performed the model simulations. TN identified the ostracods. AR organized the fieldwork to collect the Tislit core. All authors contributed to the discussion and to improving the manuscript.

## Figure Legends

1. **Figure 1**. Maps showing the location of Lake Tislit, core GC2711, and Lake Yoa6, along with the schematic position of the Inter Tropical Convergence Zone, with modern mean (A) summer (JJA) and (B) winter (DJF) rainfall56. Map (C) shows the correlation coefficients between Tislit and northern Morocco for winter precipitation (DJF) variability over the 1901-2010 time period.
2. **Figure 2**. Time series of vegetation and climate proxies obtained from Lake Tislit, and Dprecip from core GC27, located offshore of Morocco11. (a) 18O isotopes from fossil ostracods; (b) Dprecip (corrected for ice volume and temperature effects, see methods and figure S6); (c) Dprecip of core GC27, off the coast of Morocco11; (d) pollen percentages of trees and shrubs; pollen-based reconstructions of (e) annual; (f) winter (DJF; (g) spring (MAM), and (h) summer (JJA) precipitation in mm with standard deviations (gray area). All Tislit curves correspond to moving averages over three samples. The points in (a) correspond to raw data. The red bars on the Y axes of the pollen-based reconstructions (e, f, g, h) indicate the modern values. The AHP is highlighted in light blue shading. YD = Younger Dryas.
3. **Figure 3:** Zonal mean monthly precipitation (A1, B1, C1), used for simulating biomes (A2, B2, C2) and net primary productivity (A3, B3, C3) at 9 ka with the CARAIB vegetation model. The three simulations were performed using: (A) HadCM3 9 ka climatology41; (B) 300 mm precipitation added each year to modern values, only during the monsoon season, over the whole simulated area, and (C) an increase of 300 mm precipitation each year below 18°N in the summer season only, above 24°N in the winter season only, and with a progressive transition between 18°N and 24°N where precipitation occurs in both summer and winter (table S2). The data for simulations B and C are available in the supplementary information.