## Abstract

1. **The greening of the Sahara, associated with the African Humid Period (AHP) between ca. 14500 and 5000 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 realm.**
2. **In this article, we present a 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 northern Sahara 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 9ka 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 9ka. 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. 14.5ka (thousand years ago) to ca. 5ka, with an optimum between 11 and 6ka11,17.
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 8.5m long sediment core from Lake Tislit (ca. 32°N): an endoreic 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 radiocarbon dated continuous record of the last 18500 years (figure S1). Its pollen content (figure S2) shows an overall dominating Mediterranean ecosystems with arid steppe elements (*Artemisia* and Chenopodiaceae) between 18.5ka and 15ka and sclerophyllous evergreen tree and shrub taxa (*Pinus, Quercus, Olea, Pistacia*) during the AHP. After 5ka, the landscape remained dominated by pine and oak trees with a recolonization of the steppic sagebrush. Mediterranean plant species such as *Olea* and *Quercus* evergreen are adapted physiologically to summer drought24-26 and grow under a marked seasonal distribution of precipitation throughout the year (figure S3). Their spread, along with other Mediterranean plant taxa, in Tislit during the Holocene (figure S2), clearly indicates higher amounts of precipitation in winter than in summer. The Tislit pollen record allowed us, for the first time in northern Africa, to quantitatively reconstruct the seasonal changes of temperature (figure S4) and precipitation (figure 2) using the overlapping climatic ranges of pollen taxa (see methods). These climatic ranges are obtained from an extensive database of georeferenced modern plants distributions. The accuracy of the method was validated for Morocco by comparing reconstructed pollen-based precipitation from an extensive modern dataset to instrumental values (figure S5, see methods).
2. The pollen-based reconstruction shows that summer rainfall (figure 2h) did not change significantly over the past 18500 years while winter (figure 2f) and spring (figure 2g) rainfall increased by ~30% between ca. 14ka and ca. 9.5ka, reached their highest values between ca. 10.5 and 8.5ka, which corresponds to the AHP as evidenced in northern African sites10 and decreased then by ~15% until ca. 5.7ka. This result obtained from a mathematical technique quantifies the inference based on the ecological and physiological requirements of the fossil plant taxa. The increase in the annual amount of precipitation during the AHP (figure 2e) is thus robustly related to a higher contribution of winter and spring rainfall rather than to summer rainfall which remains almost unchanged during the whole period (figures 2h). Temperature has an impact on the water availability for plants through evaporation, which may affect the ecosystems composition. 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 of the water availability. Summer temperature had also a minor effect since the Mediterranean species are adapted to long lasting drought periods.
3. Stable oxygen isotopes (18O) of ostracod shells were analyzed from the Tislit core as well (see methods). Because Lake Tislit has no outlet, the 18O record (figure 2a), corrected for temperature changes, reflects variations in the lake hydrological budget. Highly depleted 18O values observed 18 to 13ka indicate a massive increase of freshwater input resulting from the melting of a glacier that was present in close vicinity of the lake27. After the disappearance of the glacier at ca. 12ka27, 18O variations reflect changes in the precipitation-evaporation budget and suggest humid conditions in the early Holocene followed by a progressive aridification trend, 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. Because it is more directly linked to precipitation and not as much influenced by evaporation, the leaf wax D record shows substantial differences with the ostracod 18O record. However, it does clearly record a period with isotopically depleted precipitation consistent with increased rainfall between 11 and 5ka.
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 amount effect of precipitation. Currently, there are three main moisture sources for Morocco: the northern Atlantic Ocean, the central Atlantic Ocean and the Mediterranean Sea29. The northern Atlantic moisture source provides the isotopically most depleted rainfall, followed by the central Atlantic and the Mediterranean source which is isotopically most enriched29. The depleted Dprecip estimates during the AHP (figure 2b) thus likely indicate a predominance of remote northern Atlantic moisture. The abrupt enrichment in Dprecip estimates at 5ka, which is not reflected in the pollen-based precipitation estimates, therefore likely was related to the sudden cooling in the North Atlantic Ocean due to a reduction in the Atlantic thermohaline circulation at that time30 which would have decreased the importance of the remote northern Atlantic moisture (isotopically depleted) in favor of the relative contributions of (isotopically enriched) proximal central Atlantic and Mediterranean 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 northern Sahara**
7. An analysis of the precipitation variability over the period 1901-2010 in Morocco shows that the winter amounts in Tislit are strongly and significantly correlated with a wider adjacent area (figure 1C) which allows us to consider that the Tislit paleoclimate record is not a local feature but is representative of the climate history of a larger region that includes at least the northwest Sahara and the Mediterranean region. In addition, the Dprecip record from Lake Tislit (figure 2b) shows a strong coherence with the Dprecip record of the marine core GC27 (figure 2c) from offshore Morocco11 (figure 1), with regards to the timing of the two depleted peaks 15-12.7ka and 11-5ka, that 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 today strongly correlated with those in the catchment that brings sediments with 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, an increase in precipitation amount in parallel with prevalence of a remote moisture source (northern Atlantic Ocean vs Gulf of Guinea) likely caused the similarity of the Dprecip records making Dprecip not indicative of specific moisture sources (summer monsoon vs winter storm tracks).
8. Numeric simulations of the Earth’s climate forced by precession changes showed 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 to a southern shift of the Hadley cell, the westerlies, and the Mediterranean storm track, bringing increased winter precipitation to Northern Africa23. Although this mechanism has a relatively small rainfall effect in Northern Africa in simulations, it is qualitatively consistent with our observations. The in-phase variability of Mediterranean winter rainfall with the Northern 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 of 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 100mm 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 to sustain a Green Sahara. Fossil pollen data indicate that the Green Sahara was composed of Sahelian biomes south of 24°N and of 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 an 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 thus 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. An environment characterized by two rainfall seasons would have thus existed during the AHP between 18°N and 24°N. The total annual precipitation in this zone likely was small, being at the boundary of both precipitation systems. However, even with low amounts, 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) length to less than 6 months instead of 10-11 months if rainfall was only 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 annual amount of rainfall over both winter and summer would sustain vegetation better than higher rainfall amount occurring in a single season which should also 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 dynamic vegetation model CARAIB (see methods) of long-demonstrated performance37-40. 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 9ka insolation and atmospheric CO2 conditions (figure 3). In simulation A, CARAIB was forced by the rainfall regime produced by the HadCM3 model palaeoclimate simulation at 9ka, and corrected for its modern biases41 (A1). Simulation A is an illustrative example of climate models early Holocene simulations. Simulations B and C are idealized scenarios to test the effect of rainfall seasonal distribution on Sahara biomes and net primary productivity (NPP) at 9ka where 300mm.year-1 were added to the modern precipitation regime over entire Northern Africa, with two different seasonal distributions. The rainfall increase of 300mm.year-1 lies within the range of quantitative estimates derived from fossil pollen records in the Green Sahara42,43. The additional precipitation annual amount was distributed in the summer season (JJA) in simulation B as a simplified representation of the hypothesis that the AHP was solely related to a strengthened African monsoon (B1). Simulation C is a test of the alternative model proposed where the additional 300 mm.year-1 were 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, including thus 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 a NPP lower than 50 g.C.m-2.yr-1 (A3). The precipitation regime produced by the HadCM3 model at 9ka fails to sustain a Green Sahara, in line with most climate system models44. Simulations B and C show both stronger 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 300mm of rainfall. This is neither compatible with vegetation reconstructed at 6ka 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 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 a theoretical progress in this experiment.
	1. The realistic Green Sahara produced by vegetation simulation C compared to B supports 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 concomitantly with a northward expansion of the summer monsoon belt. Increased winter rainfall over the northern Sahara was necessary to allow the persistence of a Green Sahara 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 usually invoked to explain the AHP in northern Africa between 14.5ka and 5ka. Isotopic and pollen evidence confirm that Morocco was wetter than today during the AHP, along with all other 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 show that the Green Sahara is best represented under 9ka conditions with Mediterranean winter precipitation penetrating southward down to 18°N while summer monsoon is shifted northward and strengthened up to 24°N. Additional climate records of seasonal precipitation amounts 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 target shift in the evaluation of IPCC Earth system models and their ability to simulate African climate variability47,48.

## Materials and methods

### Geographical settings of the Tislit record

1. Morocco is located in Northwest Africa and has vast coastal areas, a mountainous interior (Atlas Mountains) and large portions of deserted regions that extend south. Climate is Mediterranean with winter moisture transported through 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 a 8.5 meter long sediment core (32°11'N 5°38'W, 2250m asl) in 2016 under 5m 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 formed in 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 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. Today, the hills surrounding the lake are treeless except for few strands of pines (*Pinus halepensis*) and poplars (*Populus alba*) on the edge of the lake. The dominating vegetation is mainly 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 18500 years cal BP. The accumulation is continuous and rather constant in the whole core. We collected 171 samples from Tislit core in 5-cm intervals which corresponds to an average time resolution of about 100 years. Samples were then sub-sampled for pollen, ostracods for stable oxygen isotope analyses and leaf wax analyses.

### Pollen analyses

1. A set of 171 sub-samples were treated chemically for extracting their pollen content using HCl, KOH, ZnCl2 and acetolysis (sulfuric acid and anhydrid acetic). Pollen grains were identified and counted using a photonic microscope. We identified 78 pollen taxa among which 10 are aquatics. 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 is between 108 and 758 (with a mean of ca. 220). Ten samples were pollen barren among which the 7 uppermost ones (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 under marked seasonal climate such as the Mediterranean are a powerful climate proxy for evaluating the past seasonal changes of precipitation. As an illustration from the Tislit pollen data, herbs or trees such as *Asphodelus* or *Olea*, require low amounts of precipitation during summer (less than 50mm during JJA) but require more than 300mm in winter (DJF) (figure S3 and S8). Their co-occurrence in the pollen record allow to reconstructing these seasonal amounts. Conversely, the co-occurrence of taxa such as *Ilex aquifolium* and *Salix*, for instance, will reflect a lower seasonal contrast (figure S8). We describe hereafter the process of the quantitative reconstruction and its uncertainties.
2. The first step is 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 not distinguishable. Based on our palynological, botanical and ecological background, we assigned 45 pollen taxa identified in the Tislit record (table S1) to plant species that are available in a personal database which contains 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 are either aquatics, human related, with pollen percentages lower than 1% or their georeferenced modern range is not available. The plant geographical occurrences are 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 precipitation monthly values of the assigned plant species based on their modern climate ranges (figure S8). Changing contributions of species within a pollen taxon does not affect the reconstruction since the pollen taxon climatic envelope always includes the species envelope.
4. Fossil pollen samples contain different number of taxa and different taxa which express different precipitation median values from one sample to another. The reconstructed monthly precipitation value corresponds to the weighted median (pollen percentages are used as weights) of the medians of the climatic ranges of those taxa identified in a fossil sample. The reconstruction uncertainty is estimated by 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. Compared 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 co-occur only if the originating plant species have co-existed and therefore, there was an overlap of all their climatic variables. This overlap of the species climatic ranges hypothesis is valid for both modern and past ecosystems and it takes into account a potential range shift in the species realized niche57.
6. The small variation of the atmospheric CO2 during the Holocene (roughly between 250-270 ppmv)58 have had less impact on the ecosystems than during the LGM59 which should represent a negligible bias in the reconstructed precipitation values during the AHP.
7. Pollen grains disperse mainly by wind (pollen grains from entomophilous plant species are rather rare in the fossil samples) and thus some of them may be transported over long distances and affect the estimated climate. Those pollen grains usually do not exceed 1% of the total pollen sum, which is the threshold that we have used to select pollen taxa and avoid this error source in the climatic 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 are rather well correlated (r>0.6) to the observed climate. Summer reconstructed and observed precipitation are less well correlated (r=0.43) due to the low amounts of rainfall and their more stochastic occurrence. Precipitation is generally overestimated in arid areas because plants are all in the limit of their range while the method considers the optimum climate value of species as 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. 300mm.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 high specific heterogeneous environments while Tislit is a sediment record from a large lake that has integrated continuously the vegetation changes of the surrounding landscape.
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. Among the 171 samples collected from the Tislit core, 142 sub-samples of 1cm3 sediment were disaggregated in de-ionized water with detergent, then rinsed, sieved, and dried. Ostracod shells were picked, 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 for isotopic analysis. This genus was selected for its abundance all along the sediment core. By using the same taxon for isotopic analyses in the whole record, we avoid 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. Samples were dissolved in saturated phosphoric acid at 70°C in a Kiel IV carbonate device. The oxygen isotopic composition of the obtained CO2 was measured in a Thermo Delta V mass spectrometer. The analytic reproducibility (±1σ) was 0.1‰ based on long-term analysis of laboratory calcite standard samples. Isotopic values (figure 2a) are reported in permil as relative deviations 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 palaeotemperature 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. 2-3 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 internal standard. Total lipid extracts (TLEs) were dried in a Heidolph ROTOVAP system. Residual water was removed over columns of Na2SO4 using hexane as eluent. 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 over columns of AgNO3-coated SiO2 using hexane as solvent to remove unsaturated compounds. *n-*Alkanes were quantified using a Thermo Fisher Scientific Focus gas chromatograph (GC) equipped with a 30m 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-length. Repeated analyses of standard solutions indicate a quantification precision of 10 %. All samples are dominated by odd-numbered long-chain *n*-alkanes with *n*-C29 and *n*-C31 alkane being the most abundant homologues in all samples. CPI values67 of long-chain *n*-alkanes were 7.8 on average (3.6 - 15.4) indicating their origin from epicuticular waxes of terrestrial higher plants68.
2. 13C analyses of *n-*alkanes were conducted on a ThermoFisher Scientific MAT 252 isotope ratio mass spectrometer coupled via a GC-C combustion interface with a nickel catalyser operated 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 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 measurement. The difference between the long-term means and the measured standard values yielded a 1σ error of <0.3‰. Accuracy and precision of the squalane internal standard were both 0.1‰. Precision of the replicate analyses of the *n*-C29 and *n*-C31 alkane 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 analysed once, the long-term precision of the standards (0.3‰) was assumed. As 13C values of the *n*-C29 and *n*-C31 alkane 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 average propagated precision of 0.2‰ (<0.1 – 0.7). Mostly,13Cwax shows depleted 13C values, indicative of C3 plant vegetation, with the exception of the period of Heinrich event 1 (HE1, 16.1 – 14.9 ka BP) during which enriched 13C values occurred (figure S6). This is in line with the natural vegetation in Morocco which is entirely of C3 type under modern conditions. The elevated 13Cwax values duringHE1 coincide with high Poaceae abundance and could thus indicate expansion of C4 grasses around Lake Tislit under the extreme climate conditions during HE1.
3. D analyses of *n-*alkanes were conducted on a Thermo Fisher Scientific MAT 253™ Isotope Ratio Mass Spectrometer coupled via a GC IsoLink operated 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 H2 reference gas of known isotopic composition and are given in ‰ VSMOW. Accuracy and precision were controlled by a lab internal *n-*alkane standard calibrated against the A4-Mix isotope standard every six measurements and by the 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. Accuracy and precision of the squalane internal standard were 4‰ and 3‰, respectively. Precision of the replicate analyses of the *n*-C29 and *n*-C31 alkane was 1‰ on average (<1 - 5‰). For samples which could only be analysed once, the long-term precision of the standards (3‰) was assumed. As D values of the *n*-C29 and *n*-C31 alkane 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 estimate Dprecip using 13Cwax as estimate for vegetation type according to established procedures69. For comparability we use 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 Dprecip estimates for GC2711. This is due to the high altitude setting of Lake Tislit and documents 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, the marine oxygen isotope compilation of Bintanja66 with the LGM-present 18O range scaled to 1‰ VSMOW was used. This ice-volume correction has an insignificant effect for the Holocene and leads to slightly depleted Dprecip estimates for the time before 10,000 yrs ago (figure S6). In addition, we compensate 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 use the global average of 5.6‰/°C for Dprecip72. We use the winter averaged temperature (Dec - Feb) from the pollen reconstructions. The effects of the temperature compensation essentially are 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 along the classification of Henrot40, which includes 26 PFTs designed for large-scale or global applications. These PFTs are distributed in two vegetation storeys: grasses and shrubs (PFTs 1-11) in the understorey and trees (PFTs 12-26) in the overstorey. The model also performs a budget of water fluxes to evaluate the soil water amount in the root zone. Soil water deficit can induce (1) stomatal closure and reduction of photosynthetic assimilation, (2) reduction of 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. 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 inputs of the model 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. 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 with 280 ppmv of atmospheric CO2 (figure S7). The period 1901-1930 was used as reference, instead of the pre-industrial 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 20CR reanalyses (prepared by NOAA and covering the 20th century, 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 control 1901-1930 climate provide a 30-year sequence of daily values for each input climate variable of the model. After a spin-up phase, the CARAIB model was run over this series of 30 years and an average was performed 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 21000 years (with 1000 years 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 9ka experiments of HadCM3, only monthly mean data are available. The monthly anomalies are then calculated as the absolute anomaly (i.e., the difference between the 9ka simulation and the control pre-industrial simulation) for temperature, and as a combination of absolute and relative (i.e., ratio between 9ka and control) anomaly for precipitation. This combination is chosen in such a way that it favors the absolute anomaly whenever possible, except when negative precipitation tend to be produced for 9ka. In the latter situation, the weight of the relative anomaly is progressively increased73. The monthly anomalies are then simply added to the 1901-1930 monthly mean values, to yield a 30-year sequence of monthly temperature and precipitation for 9ka. The weather generator of CARAIB is then used to produce each year, from the monthly sequence, the daily values necessary for forcing the simulations. This weather generator is based on currently observed day-to-day variability of temperature (minimum and maximum) and precipitation per (geo-)climatic zone. A renormalisation 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, it should not impact significantly 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 year) is generated.
5. In the first simulation (3A), the climatic anomalies between 9ka and 0ka from HadCM3 were computed, interpolated and added to the 1901-1930 climate series, to obtain a 30-year climate series for 9ka at 0.5° x 0.5°. CARAIB was run using this climate series as input (repeated several times to relax initial conditions) together with an atmospheric CO2 of 263 ppmv, characteristics of the early Holocene58. To calculate the solar flux in CARAIB, 9ka orbital parameters were used, together with the percentage of sunshine hours.
	1. In the two sensitivity tests (3B & 3C), two 30-year climate series were constructed for 9ka by adding each year 300 mm of precipitation to the 1901-1930 series, uniformly over the whole simulated area. In the first case (B), the 300mm were distributed among 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 were distributed mostly among summer months at latitudes lower than 18°N, mostly among winter months (November to February) at latitudes higher than 24°N, and both in summer and winter between 18°N and 24°N (transition zone) (C1, table S2). CARAIB was run with these two 30-year series of climatic data under a 9ka configuration (263 ppmv of CO2 and 9ka orbital parameters).
6. For consistency, in simulations B and C, the air relative humidity r is increased and the percentage of sunshine hours s is decreased simultaneously to the increase of precipitation. 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 on the simulated areas for the period 1901-1930 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 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 are included. This yielded the following relationships allowing to calculate r and s as a function of precipitation P:
8. $r\left(P\right)=α\_{r}exp\left[β\_{r}ln\left(P+1\right)\right]$ (5 < r < 100)
9. $s\left(P\right)=α\_{s}exp\left[β\_{s}ln\left(P+1\right)\right]$ (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 :
11. $∆r=r\left(P\_{9ka}\right)-r\left(P\_{0ka}\right)$
12. $∆s=s\left(P\_{9ka}\right)-s\left(P\_{0ka}\right)$
	1. to be added to each value of r and s in the 1901-1930 time series to obtain 30-yr 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, made the figures and wrote the initial manuscript. MNEB analysed 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 for collecting the Tislit core. All authors have 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 and a schematic position of the Inter Tropical Convergence Zone with modern mean (A) summer (JJA) and (B) winter (DJF) rainfall56. Map (C) shows correlation coefficients between Tislit and northern Morocco of winter precipitation (DJF) variability over the time period 1901-2010.
2. **Figure 2**. Time series of vegetation and climate proxies obtained from Lake Tislit, and Dprecip from core GC27 located offshore 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 Morocco11, (d) pollen percentages of trees and shrubs, pollen-based reconstruction 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. 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 9ka with CARAIB vegetation model. The three simulations were performed using (A) HadCM3 9ka climatology41, (B) 300mm precipitation added each year to modern values, only during the monsoon season over the whole simulated area, and (C) an increase of 300mm precipitation each year below 18°N during the summer season only, above 24°N during the winter season only, and with a progressive transition between 18°N and 24°N where precipitation occurs during both summer and winter (table S2). Data for simulations B and C are available in the supplementary information.