Pleistocene drivers of Northwest African hydroclimate and vegetation

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Savanna ecosystems were the landscapes for human evolution and are vital to modern Sub-Saharan African food security, yet the fundamental drivers of climate and ecology in these ecosystems remain unclear. Here we generate plant-wax isotope and dust flux records to explore the mechanistic drivers of the Northwest African monsoon, and to assess ecosystem responses to changes in monsoon rainfall and atmospheric pCO2. We show that monsoon rainfall is controlled by low-latitude insolation gradients and that while increases in precipitation are associated with expansion of grasslands into desert landscapes, changes in pCO2 predominantly drive the C3/C4 composition of savanna ecosystems.

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African monsoonal rainfall has played an important role in human migration and evolution\textsuperscript{1–6} and supports agriculture and pastoralism that provides food security for at least 80 million people in the African Sahel today\textsuperscript{7}. Increasing population\textsuperscript{8} and falling crop yields spurred by decreasing precipitation and rising air temperatures\textsuperscript{9} over the last several decades has shed light on the vulnerability of this region to climate change. Wide-ranging rainfall projections for this region\textsuperscript{10–14}, increasing atmospheric pCO\textsubscript{2}\textsuperscript{15–12}, and new evidence for much greater tree cover than previously thought\textsuperscript{13} all underscore the need for improved understanding of the mechanistic drivers of this region's hydroclimate and ecosystem composition.

Several decades of work on African margin marine sediment archives of eolian dust flux demonstrate marked shifts in periodicity, from precessional (19- and 23-kyr) dust cycles during the Pliocene toward a stronger obliquity (41-kyr) component in the early Pleistocene, and ultimately to a 100-kyr beat following the Mid-Pleistocene Transition. These shifts are consistent with an increasingly strong high-latitude influence on the Northwest African monsoon. Newer Northern Hemisphere ice sheets expanded\textsuperscript{1,14,15}. Newer biomarker proxy reconstructions of Northwest African paleohydrology also show Pliocene variability dominated by precession and obliquity\textsuperscript{16,17}, when global ice volume was paced by obliquity. However, during the Middle to Late Pleistocene, when high-latitude climate is largely paced by the 100-kyr cycle, biomarker paleohydrologic records and dust flux records calculated using new constant flux proxy-normalization techniques from this region continue to be dominated by precession and obliquity\textsuperscript{16–21}. Such cycles can be driven by low-latitude insolation, latitudinal insolation gradients, or ice sheet-driven atmospheric teleconnections which climate models suggest could shape subtropical monsoon rainfall in Northwest Africa\textsuperscript{22–27}. Our understanding of these processes remains limited because only one of these late Pleistocene records extends beyond two glacial cycles, making it difficult to test the degree to which high-latitude vs. low-latitude processes drive monsoon rainfall dynamics throughout the late Pleistocene.

While rainfall regimes largely shape the distribution and ecological makeup of African savanna ecosystems today and in the past, atmospheric pCO\textsubscript{2} levels can also influence plant growth and ecosystem composition\textsuperscript{28–30}. Modern rainfall and vegetation relationships are often applied to interpret paleorecords of vegetation change as indicating changes in past hydrology\textsuperscript{16,31–33}. However, higher atmospheric pCO\textsubscript{2} levels confer competitive advantages to C\textsubscript{3} photosynthesizing plants which cannot be discerned from modern spatial relationships\textsuperscript{28,29}. Observations of savanna woody cover over the last century\textsuperscript{34–36}, CO\textsubscript{2} fertilization experiments\textsuperscript{37}, and modern vs proxy and model estimates of last glacial maximum (LGM) vegetation\textsuperscript{38,39} all show shifts toward increasingly woody savannas (C\textsubscript{3}) during intervals of higher atmospheric pCO\textsubscript{2}, independent of increasing rainfall. These results call into question the interpretation of vegetation change in Northwest Africa as a paleo-aridity indicator. Furthermore, reliable estimates of the future composition of West African savannas require improved understanding of the relative controls of rainfall and pCO\textsubscript{2} on vegetation in this region.

Here we examine the combined effects of pCO\textsubscript{2} and monsoon rainfall on savanna ecosystems and the underlying controls of high- vs low-latitude forcing of monsoon rainfall in Northwest Africa during the Middle to Late Pleistocene. We sampled marine sediment core MD03-2705 (Fig. 1a) at orbital resolution over marine isotope stages (MIS) 13 to 10 (\textasciitilde 520–360 ka), a period of dramatic changes in orbital eccentricity and the largest changes in global ice volume and atmospheric pCO\textsubscript{2} over the last 1 million years. We reconstruct monsoon intensity using both plant wax-derived δ\textsubscript{D\textsubscript{precip}} and dust fluxes normalized to the extraterrestrial \textsuperscript{3}He (\textsuperscript{3}He\textsubscript{ET}) constant flux proxy, and assess the relative controls of monsoon rainfall and pCO\textsubscript{2} on savanna ecosystem structure using plant-wax δ\textsuperscript{13}C that tracks C\textsubscript{4}/C\textsubscript{3} vegetation abundance (related to tree/grass cover in African savannas). We find that monsoon rainfall variability and dust emissions are driven primarily by low-latitude insolation gradients, and that while precipitation controls the northward expansion of grasslands into the Sahara Desert, it plays a relatively minor role compared to pCO\textsubscript{2} in controlling the composition of savanna vegetation.

Results and discussion

δ\textsubscript{D\textsubscript{precip}} reveals dynamics of Northwest African monsoon insolation forcing. Changes in monsoon rainfall inferred from δ\textsubscript{D\textsubscript{precip}} values exhibit no marked differences between glacial and interglacial intervals and rather appear more similar in pacing to changes in local summer insolation (23.5°N, June 21) (Fig. 1b). The shared variance between local insolation and δ\textsubscript{D\textsubscript{precip}} declines over time from MIS 13 to 10 as orbital eccentricity decreases, reducing the amplitude of the precession forcing, while the amplitude of the monsoon response does not change. Wavelet analysis of the δ\textsubscript{D\textsubscript{precip}} record shows the later portion of the record is dominated by obliquity pacing (Fig. 2a), while local insolation is forced exclusively by precession (Fig. 2c). The disparity between the amplitudes and the lack of strong obliquity-paced variability in the direct insolation forcing means an additional forcing mechanism is required in order to explain the variability in monsoon rainfall.

Multiple modeling studies have observed strong monsoon responses to changes in the obliquity of the Earth’s orbit\textsuperscript{22–25}. Obliquity pacing of monsoons has been hypothesized to arise via indirect control by the impact of ice sheet expansion on ventilation of cool and dry midlatitude air masses into subtropical monsoon regions\textsuperscript{22,26,40,41}, while other recent work on Northwest African monsoonal rainfall has shown that insolation gradients are a potential driver of obliquity-paced variability during the last glacial cycle\textsuperscript{42} and during the Pliocene\textsuperscript{16}. Our δ\textsubscript{D\textsubscript{precip}} record does not bear any resemblance to the high latitude temperature and ice volume evolution. The amplitude evolution of the obliquity component of the δ\textsubscript{D\textsubscript{precip}} record does not match the obliquity variability of global ice volume, and the δ\textsubscript{D\textsubscript{precip}} obliquity signal leads the ice volume obliquity signal by \textasciitilde 6 kyr, precluding ice sheets as the main driver of the observed monsoon response (Fig. S7). Therefore, obliquity pacing in our record must arise from a direct response to insolation gradients, or due to nonlinear responses to Northern Hemisphere insolation variability.

The two proposed mechanisms by which insolation gradients may force monsoon rainfall are both the result of changing heat and moisture transport from obliquity-driven changes in latitudinal insolation distributions. The first is the summer subtropical to high latitude insolation gradient, which is diminished during times of increased axial tilt resulting in decreased northward moisture transport out of the subtropics. This mechanism was originally proposed to explain obliquity-paced variability in Northern Hemisphere ice sheets both before\textsuperscript{43} and after\textsuperscript{14} the Mid-Pleistocene Transition. The second is the summer inter-hemispheric insolation gradient which links increases in monsoon rainfall during times of high obliquity to enhanced moisture transport from the South Atlantic to the Northwest African monsoon region via strengthened southerly winds associated with an intensified winter hemisphere Hadley cell\textsuperscript{22}.

Our δ\textsubscript{D\textsubscript{precip}} record is well correlated with the summer inter-hemispheric insolation gradient (23.5°N–23.5°S, June 21, r = 0.75, p < 0.001) (Fig. 1b) but has only a weak relationship with the
summer tropical to high latitude insolation gradient (25°N-65°N, June 21, $r = 0.31$, $p = 0.03$. Wavelet analysis further shows that the $\delta D_{\text{precip}}$ variability in the frequency domain is similar to the summer tropical to high latitude insolation gradient at obliquity periods (41 kyrs) but only the summer inter-hemispheric insolation gradient can explain both the precession- and obliquity-related variability in the $\delta D_{\text{precip}}$ record (Fig. 2d, e).

Previous work has attributed this dual obliquity/precession-paced variability in the northwest African monsoon to a hybrid response where changes in local insolation drive precession-paced variability, and the summer subtropical to high latitude insolation gradient drives obliquity-paced variability. Here, we find that the phasing and the scaling of the $\delta D_{\text{precip}}$ record are tightly coupled with the summer inter-hemispheric insolation gradient (Fig. 1b). It is difficult to disentangle from these data alone if increased cross-equatorial moisture transport or decreased low to high latitude moisture transport controls the obliquity response of the Northwest African monsoon. However, model simulations of increased obliquity do not show decreases in rainfall in the Northern Hemisphere extra-tropics that would result if this mechanism drove the obliquity variability. In fact, simulations of Mediterranean rainfall show in-phase responses to obliquity forcing with Northwest African monsoon rainfall indicating reduced poleward moisture transport resulting from less steep low to high latitude insolation gradients is not likely the dominant control of obliquity-paced variability of Northwest African monsoon rainfall. On the other hand, the summer inter-hemispheric insolation gradient can fully explain the monsoon response to low latitude insolation variability. The response of the northwest African monsoon can be conceptualized as a combined response to local insolation driving an increased land-sea temperature gradient and thus increased moisture transport to the monsoon region from the equatorial Atlantic, paced by precession, with a simultaneous additional response to obliquity which drives enhanced cross-equatorial moisture transport from the South Atlantic into the monsoon region. We cannot rule out non-linear responses to small obliquity-paced changes in local insolation. However, due to the agreement between our $\delta D_{\text{precip}}$ record of monsoon rainfall coupled with dynamical support for this mechanism from climate model simulations, we conclude that tropical moisture transport driven by direct thermal responses to low latitude insolation forcing coupled with summer inter-hemispheric insolation gradient driven moisture transport—not high latitude processes—is the main driver of monsoon rainfall.

**Dust flux tracks $\delta D_{\text{precip}}$.** The dust flux to our core site shows a remarkable resemblance to our $\delta D_{\text{precip}}$ record ($r = 0.70$, $p < 0.001$), tracking changes in the summer inter-hemispheric insolation gradient but not following glacial-interglacial cycles (Fig. 1b, c). Dust fluxes to marine sediments are sensitive to aridity, source area expansion, and/or wind intensity. Contraction of vegetated areas and reduced soil moisture during weak
Continuous wavelet transforms were calculated following ref. 122 with all June 21, interpolated to 3 kyr intervals. In all panels, the white parabola indicates the insolation time series sampled at wax isotope sample time points then

components of the insolation gradient can explain both the precessional and obliquity-driven

records are both faithfully recording monsoon variability.

Previous dust flux records over the Plio-Pleistocene based on age model-derived mass accumulation rates (MARs) show a strong global ice volume signature suggesting high-latitude forcing of Northwest African monsoon rainfall.13,14 However, this approach assumes sedimentation rates are uniform between age model tie points which implicitly does not account for variability in syndepositional processes including sediment redistribution (focusing/winnowing). In contrast, constant flux proxy-normalization techniques (230ThXS and 3HeET) calculate instantaneous fluxes which correct for sediment redistribution. A new 230ThXS-normalized dust record from the same core (MD03-2705) found increased spectral power for obliquity and precession compared to the age model-derived MAR technique.19 This suggests that systematic differences in sediment redistribution between glacial and interglacial intervals may have introduced unknown biases into previous age model-derived dust flux estimates. Unlike previous work which has attributed dust flux variability in this region to high latitude insolation variability, we find both the 3HeET-normalized dust flux reconstruction from this study and the 230ThXS-normalized dust flux record of ref. 20 (240–0 ka) are consistent with changes in monsoon rainfall and aridity forced by the summer inter-hemispheric insolation gradient (Figs. 3c, d and S6a, d).

C3/C4 vegetation dynamics reflect combined influence of pCO2 and rainfall. On the African continent, grassland and savanna ecosystems made up at least in part by C4 grassy vegetation exist within a mean annual rainfall range of ~250–1750 mm/yr, where woody (C3) xeric shrub vegetation dominates below this range and closed-canopy forests above it.30,48 Within these rainfall limits, the varying physiologies and growth strategies of C3 trees and C4 grasses affect their relative abundance in response to environmental conditions: C3 grasses outcompete C3 trees when growing seasons are warmer,9,50 rainfall is lower or more seasonal31, when atmospheric CO2 is lower29,49, or when disturbance by fire or herbivory is high52. Here we explore the role of changing rainfall amount and atmospheric pCO2 as potential drivers of landscape-scale C3/C4 balance.

As expected, our record shows higher δ13C values—indicating more grassy (C4) vegetation—during low pCO2 glacial intervals. While the extent of global glaciation, mostly controlled by Northern Hemisphere ice volume, is highly correlated with atmospheric CO2 levels, during glacial inceptions CO2 falls rapidly, in line with global temperature, while ice volume increases more gradually33. Our new δ13C record tracks changes in CO2, not ice volume (Fig. S8), indicating that CO2 and not the extent of glaciation is the primary driver of the observed glacial-interglacial variability in ecosystem C3/C4 balance. There is also a weak correlation indicating more grassy C4 vegetation (more positive δ13C) during high monsoon rainfall intervals (more negative δDPrecip) (Figs. 1d, S9). This relationship is counterintuitive, but has been previously described by ref. 42 as resulting from expanded grasslands into previously sparsely vegetated desert landscapes along the Southern edge of the Sahara during intervals of enhanced monsoon rainfall. During periods of higher monsoon rainfall, such as the African Humid Period18, both pollen records44,55 and model36 show C4 grasslands expand into...
from just offshore of the Congo Rainforest shows enhanced C₃ vegetation in the LGM compared to the Late Holocene. The physiological advantages that benefit C₃ vegetation during times of low atmospheric pCO₂ are likely outweighed in well-established rainforest ecosystems where out-shading by closed-canopy trees prevents grasses from proliferating despite their photosynthetic advantages. Stronger trade winds during the LGM may have increased plant-wax transport from the Congo Rainforest to the equatorial Atlantic during boreal summer causing a shift toward more negative plant-wax Δ¹³C values at this equatorial site unrelated to changes ecosystem structure. Nevertheless, these broad patterns illustrate the differential effects of pCO₂ and monsoon rainfall on grassy savanna ecosystems. Enhanced monsoon rainfall expands the northward edge of rain-limited savanna grasslands, while higher pCO₂ favors woody C₃ vegetation growth in existing savannas.

These results also corroborate similar conclusions drawn in an ecological modeling study from Southwest African savannas. This study showed that the higher reconstructed abundances of C₄ plants during the LGM in Southwest African savannas compared to the late-Holocene required plant physiological responses to CO₂ in addition to changes in monsoon rainfall and temperature. Our new data show that this CO₂-induced physiological driver of C₃/C₄ balance also holds true in Northwest Africa for at least the last ~500 ka, lending more confidence to the importance of a pCO₂ control on savanna woody cover on the African continent.

We observe different magnitudes in the response of C₃/C₄ balance to monsoon rainfall and pCO₂ during MIS 13–10 (this study) compared to MIS 5–present at site ODP 659 (adjacent to our site). During both intervals, pCO₂-driven changes are of similar magnitude. However, despite similar variability in monsoon rainfall (ΔDprecip) (Fig. 3a, b), the MIS 5–present (120–0 ka) vegetation (Δ¹³C) from core site ODP 659 appears more sensitive to changes in the monsoon than during MIS 13–10 (Fig. 3c, d, ED9). This can be explained by more northerly-shifted ecosystem boundaries during MIS 13–10, which is supported by pollen reconstructions. During MIS 13-10, closer proximity of the core sites to savanna ecosystems where woody (C₃) vegetation growth is restricted under lower atmospheric pCO₂ results in a greater impact of pCO₂ compared to rainfall on the regional C₃/C₄ balance.

Implications for the future of Northwest African ecosystems. The combined records of ΔDprecip and plant-wax Δ¹³C presented here show that since at least ~500 ka the physiological control of atmospheric pCO₂ on photosynthesis dominantly controls the woody/grassy balance in existing savannas, while the largest effect of increased monsoon rainfall on Northwest African vegetation is to expand C₄ grasslands into the Sahara Desert. This is consistent with recent results suggesting pCO₂ has likely played an important ecological role in the vegetative evolution of Africa during the LGM-Holocene and over the Neogene. The new insights from our record suggest that since pre-industrial times, rising atmospheric CO₂ concentrations have likely been a strong forcing on woody cover in African savanna ecosystems, corroborating observational studies over the past several decades which attribute current increasing trends in African savanna woody cover with rising CO₂ levels. However, controlled CO₂ release experiments reveal that the effect of CO₂ fertilization on woody cover is non-linear and likely saturates at values higher than ~400–500 ppm, which makes the future ecological role of atmospheric CO₂ in savanna ecosystems uncertain. Nevertheless, persistently high concentrations of CO₂ (~400 ppm) in the atmosphere will impose a continued ecological pressure favoring previously unvegetated areas, increasing the overall area covered by C₄ plants.

The relative expression of CO₂-driven changes in savanna C₃/C₄ makeup and monsoon rainfall-driven expansion of C₄ grasslands into unvegetated areas recorded by plant-wax Δ¹³C will depend upon where a core site is located in relation to existing ecosystem boundaries. Expanding upon previous work, we have compiled plant-wax Δ¹³C data from core top and downcore records along the West African margin to assess the spatial relationship between the pCO₂ and monsoon rainfall on landscape C₃/C₄ balance (Fig. 4). In comparison to the drier late Holocene (2–0 ka), sediments from the wetter middle Holocene (8–6 ka) have more positive plant-wax Δ¹³C values poleward of ~15°N, consistent with C₄ grass expansion into the Sahara Desert. Mid-Holocene C₃ woody contributions increase at equatorial latitudes consistent with poleward movement of the forest/savanna boundary (Fig. 4a, b). During the LGM (23–19 ka), when atmospheric CO₂ concentrations were ~90 ppm lower but rainfall as estimated by plant-wax ΔD₂¹H, runoff from the Niger River, and paleolake levels were broadly similar to modern (see methods for more details), at nearly all latitudes there is a higher proportion of C₄ plants compared to the late Holocene (Fig. 4c, d). One sediment core...
tree over grass growth. The abatement of woody encroachment on savannas will thus be a more difficult task, posing distinct challenges to agropastoralist communities that rely on savanna ecosystems for livestock grazing.

Methods

Site, samples, and source region. The IMAGES Calypso core MD03-2705 was taken in the eastern equatorial Atlantic off the Mauritian Coast (18°05′ N, 21°09′W) at a water depth of 3085 m below sea level67. The core site is located at the apex of a 300 m seamount between the Cape Verde Islands and the North Atlantic margin and is under the direct influence of the present-day Saharan dust supplies68. Regarding this particular bathymetric and geographical setting, previous work has shown that non-carbonate silicilastic input69, as well as plant waxes, are primarily delivered to core sites in this region by easterly winds from the adjacent Western African continent with dust sources constrained to the western and central Sahara70 and plant waxes constrained to the African continent primarily from South of the Sahara (see “Interpretation of plant-wax isotopes” section below for details) (Fig. 1). The core was sampled to target precession cycles and magnetic reversals provide additional age control in the lower portion of the core70. The corresponding to the lower and upper Jaramillo and the Matuyama/Bruhnes transitions of the geomagnetic polarity time scale70.

Age model. The age model for core MD03-2705 was determined via peak-to-peak matching of the benthic foraminifer 210Pb record from this core70 to the LR04 global benthic stack71 (Fig. S1, Supplementary Data 1). Three paleomagnetic reversal ages were used: (a) lower and upper Jaramillo and the Matuyama/Bruhnes transitions of the geomagnetic polarity time scale70, (b) another peak peak matching of the benthic foraminifer 210Pb record from this core70 to the LR04 global benthic stack71 (Fig. S1, Supplementary Data 1), (c) another peak peak matching of the benthic foraminifer 210Pb record from this core70 to the LR04 global benthic stack71 (Fig. S1, Supplementary Data 1). Three paleomagnetic reversal ages were used: (a) lower and upper Jaramillo and the Matuyama/Bruhnes transitions of the geomagnetic polarity time scale70, (b) another peak peak matching of the benthic foraminifer 210Pb record from this core70 to the LR04 global benthic stack71 (Fig. S1, Supplementary Data 1), (c) another peak peak matching of the benthic foraminifer 210Pb record from this core70 to the LR04 global benthic stack71 (Fig. S1, Supplementary Data 1). Three paleomagnetic reversal ages were used: (a) lower and upper Jaramillo and the Matuyama/Bruhnes transitions of the geomagnetic polarity time scale70, (b) another peak peak matching of the benthic foraminifer 210Pb record from this core70 to the LR04 global benthic stack71 (Fig. S1, Supplementary Data 1), (c) another peak peak matching of the benthic foraminifer 210Pb record from this core70 to the LR04 global benthic stack71 (Fig. S1, Supplementary Data 1).

Plant-wax n-alkane biomarker extraction and quantification. Sediment samples were freeze-dried and lipids were extracted from ~20 g dry and crushed sediment aliquots using a Dionex 200 Accelerated Solvent Extractor (ASE) using DCM:methanol (9:1 v/v). Total lipid extracts (TLEs) were spiked with an internal recovery standard and integrated using Chemstation (Agilent) software. Concentrations of n-alkanes were determined by comparison to an internal 5α-androstan-3α-ol recovery standard using a response factor for the ion m/z 57 calculated from an external standard mixture of C15–C35 n-alkanes run every six samples. Concentrations of long-chain (C35–C37) n-alkanes displayed high odd-over-even preference (5.80–7.54) with a maximum peak at C37 consistent with a terrestrial plant biomarker source. Concentrations were further used to determine dilution volumes for each sample before compound-specific carbon and hydrogen isotope analysis. All concentrations can be found in Supplementary Data 2.

Compound specific n-alkane δD and δ13C. Compound specific carbon (δ13C) and hydrogen (δD) isotope measurements on n-alkanes in the aliphatic organic fraction were performed using a Thermo Delta V Advantage isotope ratio mass spectrometer coupled to a Thermo Trace GC Ultra and Isolink through a ConFlo IV. Each sample in 1–4 μl of hexane was injected into a PTV injector with 2 mm i.d. silica-tailed packed with glass wool. The inlet was run in splitless mode at 60 °C during the injection then ramped to 320 °C and held for 1.5 min during the transfer phase. Separations of individual n-alkanes were done on an HP-5MS column (30 m length, 0.25 mm i.d., 0.25 μm phase thickness) with a constant helium flow of 1.0 ml/min. The GC oven settings were as follows: 60 °C hold of 1.5 min ramped at 15 °C/min to 150 °C and then at 4 °C/min to 320 and held for 10 min.

Carbon isotopic compositions of n-alkanes were measured via combustion to CO2 after chromatographic separation via a custom-made combustion reactor consisting of one strand each of nickel, copper, and platinum wires inside a 0.5 mm i.d. fused alumina tube placed on a hot plate and a 1 k 1 % of O2 in He was introduced inline prior to the combustion reactor to ensure continued oxidation and complete combustion of compounds. Simultaneous measurements of n-alkanes of known carbon isotopic composition (purchased from Arndt Schimmelmann, University of Indiana) were performed between every six samples to determine individual compound δ13C values on the VPDB scale.

Hydrogen isotopic compositions of n-alkanes were measured via pyrolysis to H2 via a rctor purchased from Thermo-Fisher Scientific consisting of a 0.5 mm i.d. fused alumina tube connected to the GC oven through a stainless steel column. The reactor was conditioned with two injections of 1 μl hexane. Simultaneous measurements of n-alkanes of known hydrogen isotopic composition (purchased from Arndt Schimmelmann, University of Indiana) were performed between every six samples to determine compound δD values on the VPDB scale. Replicates of every sample for both hydrogen and carbon analysis were run to assess reproducibility. Conversion of δ13C and δD to the VPDB and VSMOW scales respectively and their uncertainties were calculated following ref. 72.

Interpretation of plant-wax isotopes. Change in the δ13C of atmospheric CO2 can bias estimates of plant-wax δ13C across glacial transitions. A recent compilation of δ13C CO2 over the last 150 kyrs encompassing the last glacial cycle found variability of only ~0.5% between glacial and interglacial conditions, with more enriched δ13C CO2 during glacialis (LGM and MIS 4) and more depleted δ13C CO2 during interglacials (Holocene, MIS 3, MIS 5d)74. Direct measurements of δ13C CO2 variability across MIS 13–10 have not been made, however, seem unlikely to have
varied much more than over the last glacial cycle given the similarities in pCO2 change across this interval. Here, plant-wax δ13C values are not corrected for changes in δ13Cwater which would result in interglacials and more positive values during glacials, and thus the record we present here is a conservative estimate of changes in vegetation during this interval.

The plant-wax δD record of the C3 n-alkane was corrected for changes in δ18Owater across MIS 13–10 following ref. 25 by scaling the LR04 benthic δ18O stack27 of the depth 

\[
\delta D_{\text{wax,IPC}} = (\delta D_{\text{wax,IPC}} + 1)/(\delta D_{\text{wax,IPC}} - 1)
\]

The ice-volume corrected plant-wax δD record (\(\delta D_{\text{wax,IPC}}\)) was then calculated with the following equation:

(1)

The carbon isotope composition (δ13C) of plant waxes deposited in marine sediments in the eastern Atlantic is sensitive to plant physiology in Western Africa, namely the photosynthetic pathway used by the wax producer for fixing organic carbon (e.g., C3, C4)76. Here, we interpret changes in the plant-wax δ13C as primarily representative of changes in the percent landscape cover of C3 grass v. C4 trees using the δ13C of the C3, n-alkane26, but changes in local hydrology, temperature, and pCO2 can all potentially impact the δ13C of plant waxes.

The provenance of the plant waxes at our study site has important implications for the interpretations of our paleoceanography and paleohydrology reconstructions. The range of the plant-wax (C3, n-alkane) values presented here (~25.98 to

\[\delta D_{\text{wax,IPC}} = (\delta D_{\text{wax,IPC}} + 1)/(\delta D_{\text{wax,IPC}} - 1)\]

The same data have been used to argue for a greater contribution of Med source plant-waxes offshore Northwest Africa during weak monsoon intervals42,54. Within this framework, plant waxes at our core site should reflect changes in the vegetation zones south of the Sahara Desert as well as variation in trade wind strength, influencing the amount of waxes transported from the Med source. Strong trade winds would deliver C3 plant waxes and lead to more overall negative δ13C wax values with savanna source C3/C4 vegetation changes superimposed. The effect of the Med source would be most pronounced during weak monsoon intervals when there is reduced vegetation cover in the savanna source region, and therefore the Med source makes up a larger proportion of the total wax flux. During periods of greater transport of Med source plant waxes, weak monsoon intervals will have more negative wax δ13C values reflecting the increased proportion of Med source C3 waxes.

A pollen reconstruction extending beyond the LGM at ODP 659 (adjacent to our core site) shows much higher fluxes of trade wind indicator pollen between 700 and 300 ka compared to the last ~130 ka suggesting stronger trade winds during our study interval11 of MIS 13–10. This agrees well with the higher dust fluxes, sensitive to trade wind strength, found in this study. These stronger trade winds would increase the flux of C3 plant waxes from the Med source and increase the amplitude of δ13C wax values. During weak monsoon intervals, the Med source increases the overall C3 contribution to our core site leading to more negative δ13C values. During strong monsoon intervals, the effect of increased transport of C3 waxes from the Med source would be muted by the expanded C4 grasslands. The effect of this is an increased amplitude of δ13C change without any change in the vegetation response to orbitally driven monsoon changes. Therefore, we expect a stronger relationship between δDprecip and the Med source during MIS 13-10 compared to during the past ~130 ka. However, we find the opposite. The relationship between δD and δ13C is strongest for the last 130 ka and weaker for MIS 13-10.

An alternative scenario, and the one favored here, is that the C3 source to our core site is predominantly the savanna source to the south. The increased C3 component observed during weak monsoon intervals is not the result of increased transport of waxes from the Med source, but rather the result of the reduced area of C4 grasses. Further evidence for this interpretation comes from pollen reconstructions of this region which display the Middle Pleistocene transitions which show more northerly excursions during MIS 13-10 by several degrees of latitude compared to the last glacial cycle83. During MIS 13-10 when ecosystem boundaries were farther northward, the wax-shed of our core site would have been composed of a smaller area of desert ecosystems and a greater area of grasslands, as well as deciduous woody/grassy savannas, and Sudanian deciduous forests. At this time, increased rainfall would have led to expanded grasslands increasing C4 plants, but also increased woody cover in savannas and to a lesser degree expanded deciduous forests which would cause a simultaneous rise in C3 plants in the wax-shed resulting in a more muted increase in the C3 character of the waxes than during intervals when ecosystem boundaries were farther southward (e.g., the last ~130 ka). An additional consequence of these more northerly ecosystem locations is that a greater percentage of the wax-shed is constituted by mixed woody/grassy savannas, making the δ13C record of this interval particularly sensitive to vegetation changes in these ecosystems. The differences in variance in the δ13C records explained by monsoon rainfall change and atmospheric CO2 concentration can be understood within this framework. During the last ~130 ka, the Sahara Desert extended farther southward. Thus, the wax-shed was more strongly influenced by changes in the northward extend of grassland shifting into the desert during times of increased rainfall and secondarily by changes in the woody cover in savannas resulting from glacial-interglacial palaeoclimatic changes85–88.

The hydrogen isotope composition (δD) of plant waxes is more directly linked with changes in local hydrological conditions because the source of hydrogen in wax compounds is local precipitation water86 which have been shown to be dominantly controlled in this region via the amount effect: Rayleigh fractionation46. Further, more depleted hydrogen isotopes are more depleted in rainfall increases83–88. Biosynthesis of plant waxes imparts an additional apparent fractionation (\(\epsilon_a\)) on the hydrogen isotopic composition of plant waxes relative to the source water that is dependent on the plant photosynthetic pathway84. To calculate the hydrogen isotopic composition of precipitation (δDprecip) the apparent fractionation factor (\(\epsilon_a\)) for each sample must be estimated based on the fraction of C3 and C4 photosynthesizers present in the landscape. The fraction of C3 contribution to our C3 n-alkane record was calculated using a linear mixing model between δ13C values of the C3 n-alkane for C3 (δ13C = −9.9‰) and C4 (δ13C = −33.6‰) plant end members for the African continent calculated from a compilation of measurements of modern plants79,80 following:

\[
f_{C3} = \left( \frac{\delta D_{\text{wax,IPC}} - \delta D_{\text{wax,IPC,c3}}}{\delta D_{\text{wax,IPC,c4}} - \delta D_{\text{wax,IPC,c3}}} \right) + 1 \quad \text{and} \quad f_{C4} = 1 - f_{C3}
\]

(2)

(3)

Here we interpret the calculated δDprecip as qualitatively representative of changes in the amount of monsoon precipitation (i.e., wet season rainfall).

Recent work has shown that orbital scale variability in winter season rainfall in the Mediterranean region likely contributed to the northward expansion of grassland and savanna ecosystems during Green Sahara episodes93, however the δDprecip in North Africa during humid intervals is ~10‰ more positive than at our core site94; therefore any contribution of waxes to our study site from this source would act to slightly dampen the observed δDprecip monsoon signature. During arid intervals when pollen suggests an increased northerly source, δDprecip Values are similar in both locations, suggesting a minimal effect on the δDprecip record. Thus, any Med source contribution would act to only slightly dampen the amplitude of the δDprecip record and thus inferred monsoon rainfall variability. We, therefore, as for our carbon isotope record, interpret the δDprecip variability to primarily reflect changes in wet season rainfall in the grasslands, savannas, and deciduous forests south of the Sahara, and to a much lesser extent the steppes and Mediterranean forests north of the desert on orbital timescales.

### Assessing evidence of hydrologic change during the Last Glacial Maximum

Proxy records of the hydrological conditions during the LGM (~23–19 ka) in western equatorial and northern Africa generally consist of reconstructions either directly sensitive to changes in precipitation relative to evaporation (P–E) or indirectly sensitive to continental aridity via inferred relationships between terrestrial vegetation and hydroclimate. Along the northwest African margin, marine core records of continental margin derived (CMR) monsoon hydrogen isotope records (similar and in some locations more negative) values of precipitation hydrogen isotopes from ~15–31°N between the LGM and the late-Holocene82,84 indicating similar
if not more intense monsoon rainfall during the LGM. Lake level reconstructions from across the Sahara Desert—the most direct evidence for changes in P—reveal a pattern of comparable or wetter conditions in the vicinity of lakes displayed high or medium lake levels during the LGM compared to the late-Holocene117. In contrast, utilization of a constant concentration of3He/4He end member is spatially consistent and taken to be 2.4 × 10−8 (see next section for details). Extraterrestrial3He concentrations are determined using a Monte Carlo approach (see next section for details). Dust fluxes between age model tie-points. However, these model-derived flux records must assume constant fluxes between age model tie points and may be inflated or deflated by the effects of sediment winnowing.5,118,119 In contrast, utilization of a constant flux proxy allows for point-by-point determination of vertical sediment fluxes that are independent of lateral sediment transport.

Helium isotopes were measured in carbonate-free sediment samples. To remove calcium carbonate, sediment samples were first leached in 25–30 ml of 10% acetic acid under light agitation overnight. Acidic solutions were then rinsed with MQ water and centrifuged for 5–10 min at 1370 g three times. Samples were then left to evaporate overnight before freeze-drying. The helium was extracted from freeze-dried samples via heating at a furnace at ~1300 °C and measured on an MA-25 mass spectrometer125. Helium isotopes found in marine sediments represent a combination of terrestrial and extratropical input. Measured 3He concentrations were converted to mass accumulation rates following the mass of sediments accumulated between age model tie-points. However, these model-derived flux records must assume constant fluxes between age model tie points and may be inflated or deflated by the effects of sediment winnowing.5,118,119 In contrast, utilization of a constant flux proxy allows for point-by-point determination of vertical sediment fluxes that are independent of lateral sediment transport.

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Author contributions

N.A.O. and C.S. performed the analyses; D.M., G.W., P.J.P., and C.S. conceived the study, N.A.O. wrote the initial draft of the manuscript, and N.A.O., C.S., D.M., G.W., A.J.M.B., L.L., B.M., and P.J.P. wrote the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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