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Notes

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ABSTRACT

Intense debate surrounds the evolution of grasses using the C_4 (Hatch-Slack) photosynthesis pathway and the emergence of African grasslands, often assumed to be one and the same. Here, we bring new insights with the combination of plant leaf wax carbon isotopic composition ($\delta^{13}C_{wax}$) and pollen data from marine sediments of the Gulf of Aden (northeast Africa), which show that C_4 biomass increases were not necessarily associated with regional grassland expansion. We find broadly opposing trends toward more enriched $\delta^{13}C_{wax}$ values and decreased grass pollen proportions between 12 and 1.4 Ma. This apparently contradictory evidence can be reconciled if a greater proportion of the Late Miocene northeast African landscape were covered by C_3 grasses than previously thought, such that C_4 grasses and shrubs replaced a C_3 ecosystem including trees and productive grasslands. In addition, $\delta^{13}C_{wax}$ and pollen both indicate that true rainforests were unlikely to have been extensive in northeast Africa at any time in the last 12 m.y., although seasonally dry forests were a significant component of the regional landscape since the Late Miocene. Here, we extend regionally integrative marine archives of terrestrial vegetation back to 12 Ma, and we evaluate them in the context of an updated compilation of pedogenic carbonate $\delta^{13}C$ values from East African Rift strata. We identify two distinct phases of increasing C_4 biomass between 11 and 9 Ma (with a reversal by 4.3 Ma) and then a re-expansion between 4.3 and 1.4 Ma; surprisingly, neither was associated with grassland expansion.

INTRODUCTION

C_4 plants presently thrive in low- and mid-elevation sites in tropical climates with high temperatures and warm-season precipitation (Sage, 2004); however, this was not always the case. Today, the C_4 pathway appears in >19 families; most are grasses, followed by sedges and some dicotyledons (e.g., in the Amaranthaceae family). Evidence for C_4 evolution and expansion comes from rare plant macrofossils (Tidwell and Nambudiri, 1989), modern genetic population distributions (Edwards and Smith, 2010), and most commonly from stable carbon isotope records around the world (e.g., Cerling et al., 1997). These various lines of evidence indicate that C_4 plants appeared in the Oligocene but flourished only later in the Miocene. Reasons for this expansion are currently debated (see Edwards et al., 2010) but the ecological implications of C_4 plants and their rise to dominate some ecosystems is important for understanding terrestrial biospheric systems and the evolution of grasslands.

In northeast Africa (area shown in Fig. 1), there has been intense interest in reconstructing vegetation associated with the fossil record of faunal evolution preserved in the East African Rift system. In particular, questions center on the extent of forest versus grassland habitats (Cerling et al., 2011) and the incorporation of C_4 plants into diet (Uno et al., 2011). Palynological data indicate the presence of extensive grasslands during the Miocene and Pliocene (Bonnefille, 2010); however, because C_3 and C_4 grasses cannot be distinguished on the basis of pollen morphology, increases in C_4 biomass have to be assessed by isotopic means (e.g., Cerling et al., 2011).

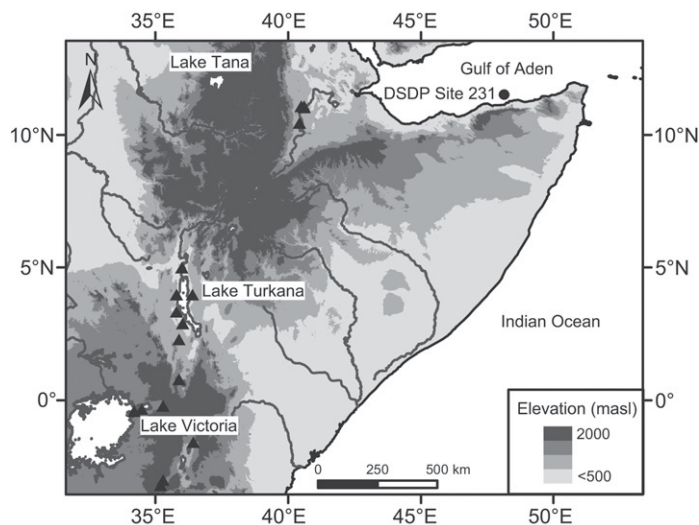


Figure 1. Location of Deep Sea Drilling Project (DSDP) Site 231 in the central Gulf of Aden (circle; 11.89°N, 48.25°E, 2152 m water depth, DSDP Leg 24) and of strata sampled for pedogenic carbonates (triangles); topography plotted from Shuttle Radar Topography Mission (SRTM) digital elevation data (Jarvis et al., 2008). masl—meters above sea level.

C_4 photosynthesis has a distinct carbon isotopic fractionation relative to C_3 plants using the Calvin cycle alone, such that isotopic measurements can identify the appearance of C_4 vegetation in the geologic record. Carbon isotopic analyses have been applied to a range of substrates, including carbonates in paleosols (Wynn, 2000), the fossil teeth of mammalian herbivores (Uno et al., 2011), and plant leaf waxes in sedimentary deposits (Schefuss et al., 2011). The carbon isotopic compositions of pedogenic carbonates ($\delta^{13}C_{pc}$) capture local variations in the distribution of woody cover where paleosols form (Cerling et al., 2011), and have been used to show Late Miocene expansion of C_4 grasslands in some regions (e.g., Quade et al., 1989). The carbon isotopic composition of fossil teeth ($\delta^{13}C_{tooth}$) also provides perspective on C_4 distributions, but through the filter of animal dietary preferences. Early studies of $\delta^{13}C_{tooth}$ records suggested that C_4 vegetation expanded in a step shift between 8 and 6 Ma (Cerling et al., 1997), but subsequent studies have shown that a shift toward a C_4 -dominated diet occurred as early as 9.9–9.6 Ma in equids, followed by rhinocerotids at 9.6 Ma, hippopotamids and bovids at ca. 7.4 Ma, and suids between 6.5 and 4.2 Ma (Uno et al., 2011). The staggered timing of dietary shifts reveals ecological complexity but leaves open intriguing questions about the nature and timing of C_4 expansion in the landscape.

With the development of compound-specific isotopic analysis and its application to plant leaf waxes, plant leaf wax carbon isotopic composition ($\delta^{13}C_{wax}$) data have been reported from lake cores (e.g., Sinnighe Damsté et al., 2011) and marine sediments (e.g., Schefuss et al., 2011) spanning the last glacial cycle. In this paper, we extend this approach to much older marine sediments from Deep Sea Drilling Project (DSDP)

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Site 231 in the Gulf of Aden in northeast Africa (Fig. 1). Marine sediments downwind from northeast Africa provide a regionally integrative and continuous archive of the terrestrial environment. Terrigenous proxies including dust (deMenocal, 1995), pollen (Bonnefille, 2010), and plant leaf waxes (Feakins et al., 2005) have already provided evidence for environmental change from this site.

Here, we extend our initial report of $\delta^{13}\text{C}_{\text{wax}}$ values from DSDP Site 231 across 11.3–1.4 Ma (Feakins et al., 2005) and provide a novel synthesis with pollen data from the same marine sediments. The combined isotopic and palynological approach enables differentiation of C_3 versus C_4 contributions to grass pollen and also allows us to evaluate how different types of C_3 ecosystems (rainforests versus seasonally dry woodlands) influenced the carbon isotope record. The continuous record of marine sedimentation permits direct comparison of the magnitude of Miocene and Pliocene C_4 expansions. We further compare the marine archive to soil carbonates in the East African Rift in order to understand the distribution of vegetation change.

MATERIALS AND METHODS

We report a 12 m.y. leaf wax record of vegetation change from marine sediments of DSDP Site 231. In an earlier publication (Feakins et al., 2005), we presented 97 analyses from discrete time slices. Here we add 255 additional analyses extending upon these time windows with samples that integrate 2–3 k.y., as well as samples that integrate 300 yr during the Miocene for direct comparison with pollen analyses (Bonnefille, 2010). Molecular-level biomarker isotopic data were collected on fatty (alkanoic) acids as their corresponding fatty acid methyl esters using a gas chromatograph–isotope ratio mass spectrometer (GC-IRMS) and $\delta^{13}\text{C}$ data are reported for the C_{30} *n*-alkanoic acid (Feakins et al., 2005). Age control is provided by an updated tephrostratigraphic and nannofossil age model for the core. Details of the method and age model may be obtained from the GSA Data Repository^{1,2}.

Plant proxy $\delta^{13}\text{C}$ values are commonly interpreted in terms of percentages of C_4 vegetation using a mixing model approach, although the range of isotopic values in bulk plant tissues results in large propagated uncertainties. Working around these issues, Cerling et al. (2011) recently introduced an algorithm to calculate fraction of woody cover, trained on a modern survey of woody cover and area-weighted mean $\delta^{13}\text{C}$ values of soil organic matter. While this approach is useful it does not differentiate between rainforest and seasonally dry trees, each of which may reach 100% canopy cover; here we explicitly test for the presence of rainforest taxa in the pollen record from the marine core. Secondly, this approach does not consider that open-canopy environments can be dominated by C_3 grasses, as may have been the case in the Miocene. For this reason we suggest that a paired pollen and carbon isotope approach is needed to reconstruct Middle to Late Miocene environments.

RESULTS AND DISCUSSION

$\delta^{13}\text{C}_{\text{wax}}$ values from DSDP Site 231 range between -31.1‰ and -22.3‰ (Fig. 2). The most negative values are reported at 11.1 and 4.3 Ma, and the most positive values at 1.4 Ma. There is a 4.4‰ positive shift in $\delta^{13}\text{C}_{\text{wax}}$ between 11.1 and 8.7 Ma, and a gradual further increase

¹GSA Data Repository item 2013079, detailed methods section (Appendix DR1), age model (Table DR2), pollen counts (Table DR3), leaf wax carbon isotopic data (Table DR4) and soil carbonate references (Appendix DR5), is available online at www.geosociety.org/pubs/ft2013.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

²Leaf wax carbon isotopic, pollen, and age model data for Deep Sea Drilling Project (DSDP) Site 231 can also be found at the National Climatic Data Center (National Oceanic and Atmospheric Administration): ftp://ftp.ncdc.noaa.gov/pub/data/paleo/contributions_by_author/feakins2013/feakins2013.txt, and ftp://ftp.ncdc.noaa.gov/pub/data/paleo/contributions_by_author/feakins2013/feakins2013.xls. The soil carbonate compilation is published at the Integrated Earth Data Applications (IEDA) EarthChem data repository: doi:10.1594/IEDA/100231.

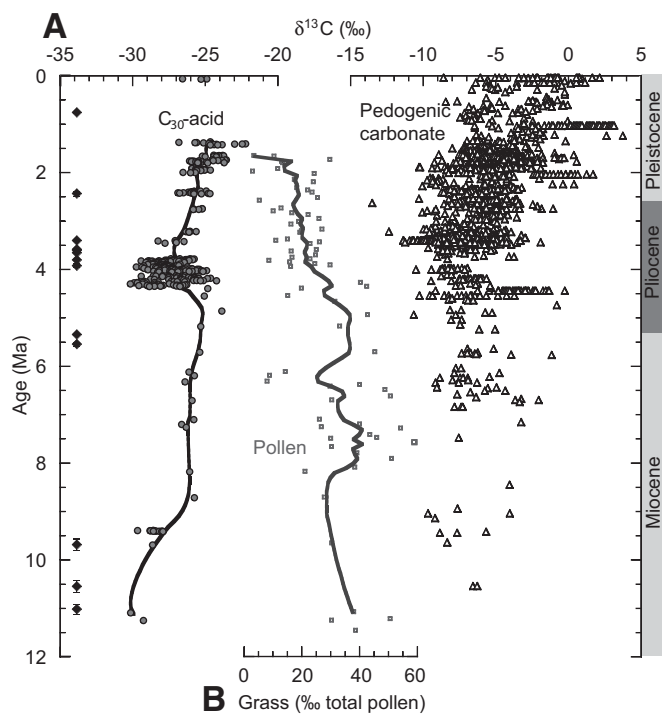


Figure 2. Carbon isotopic and pollen evidence for northeast African vegetation. A: Leaf wax $\delta^{13}\text{C}$ (circles; this study and Feakins et al., 2005; smoothing 30%) from marine sediments of Deep Sea Drilling Project (DSDP) Site 231 (location shown in Fig. 1), and pedogenic carbonate $\delta^{13}\text{C}$ (triangles; for references see the Data Repository [see footnote 1]) from East African Rift locations shown in Figure 1. All carbon isotopic data are reported relative to Vienna Pee Dee belemnite (VPDB). **B:** Grass pollen (Poaceae) as a percent of total pollen (squares; smoothing 30%) from marine sediments of DSDP Site 231 (Bonnefille, 2010; and this study). Tephra and nannofossil datums providing age control for DSDP Site 231 (black diamonds) are shown adjacent to y axis.

of 1.9‰ by 4.9 Ma, followed by a 6.3‰ decrease in $\delta^{13}\text{C}_{\text{wax}}$ values by 4.3 Ma. Higher sampling resolutions reveal variability within 10^4 – 10^5 yr cycles of up to 5‰, best sampled between 4.3 and 3.8 Ma. In addition to the cyclicity, between 4.3 and 1.4 Ma, $\delta^{13}\text{C}_{\text{wax}}$ values display an overall trend toward more positive values.

In the terrestrial archives, Miocene data are sparse and the strongest signal is a trend to more positive $\delta^{13}\text{C}$ values after 4.3 Ma where most pedogenic carbonate samples are reported (Fig. 2). This positive trend is evident amidst scatter of up to 11‰ in $\delta^{13}\text{C}_{\text{pc}}$ values at any one time interval that reflects spatial variations in vegetation as fine as 1 m^2 , including the continued presence of C_3 plants.

We view ecological change in northeast Africa as the primary driver of the $\delta^{13}\text{C}_{\text{wax}}$ and $\delta^{13}\text{C}_{\text{pc}}$ records and interpret these data as functions of the influence of C_4 vegetation on the landscape and the environmental conditions in which these plants grew. While $\delta^{13}\text{C}$ values of atmospheric CO_2 ($\delta^{13}\text{C}_{\text{CO}_2}$) can influence the $\delta^{13}\text{C}$ values of plants, benthic foraminiferal constraints on $\delta^{13}\text{C}_{\text{CO}_2}$ variability (Tippie et al., 2010) indicate that this effect is of minor importance before the Pleistocene glacial cycles in our record. Both $\delta^{13}\text{C}_{\text{wax}}$ and $\delta^{13}\text{C}_{\text{pc}}$ records show the presence of C_4 vegetation since at least 9 Ma, a minimum in $\delta^{13}\text{C}$ values in the early Pliocene (ca. 4 Ma), and an increase in C_4 vegetation through the Pliocene and Pleistocene.

Palynology provides an important link to the species responsible for the carbon isotopic signals. We find that the diversity of plant species recorded in the marine sediments of DSDP Site 231 has remained largely unchanged across the last 12 m.y., but the proportions have shifted (Bonnefille, 2010; and this study). Of greatest relevance here, grass pollen

ranges between 3% and 59% of total pollen, and displays a decline from 11.5 to 8 Ma, an increase around 8 Ma, and then an overall proportional decline from 8 to 1.6 Ma (Fig. 2). Declines in grass pollen occurred while $\delta^{13}\text{C}_{\text{wax}}$ values increased toward greater C_4 biomass proportions, indicating that gains by C_4 grasses were outpaced by losses of C_3 grasses. Gains by C_4 grasslands are further minimized if we consider that Amaranthaceae (shrubs) may be responsible for some fraction of C_4 biomass expansion.

Between 11.1 and 8.7 Ma, $\delta^{13}\text{C}_{\text{wax}}$ values increased by 50% of their full range, which is broadly consistent with a 50% increase in C_4 biomass. The timing of C_4 increase in the marine record corroborates the timing of the Miocene C_4 expansion in the diets of equids, the first responders amongst the sampled fauna (Uno et al., 2011), and confirms a significant expansion of C_4 biomass in northeast Africa by 9 Ma which is not evident in the $\delta^{13}\text{C}_{\text{pc}}$ record.

Pollen evidence has already suggested an absence of closed rainforest at East African hominin sites of Pliocene–Pleistocene age (Bonnefille, 1995) and from marine archives back to 12 Ma (Bonnefille, 2010; and this study). However this is in apparent contrast with molecular clock estimates for rainforest fragmentation and the isolation of West and East African rainforest taxa at ca. 8 Ma (Couvreur et al., 2008). In this study, we find $\delta^{13}\text{C}_{\text{wax}}$ values vary between -30.2‰ and -25.4‰ from 12 to 5 Ma, inconsistent with modern rainforest values of $\sim -38\text{‰}$ (Vogts et al., 2007). Furthermore the pollen assemblages do not include humid Guineo-Congolian rainforest taxa, most likely indicating that a geographically restricted East African rainforest lay outside the source area for leaf wax and pollen.

Reconciling the data from multiple proxies requires consideration of how each proxy may record different aspects of the regional climate and environmental system. In the Gulf of Aden there are no significant fluvial inputs; terrigenous inputs are instead windblown (Fig. 1). Low-level winds follow the topographic barrier of the Ethiopian highlands, with high elevations in place since at least 12 Ma (Wichura et al., 2010) and similar-to-modern atmospheric circulation since at least 8 Ma (Sepulchre et al., 2006), although uplift and rifting continues (Trauth et al., 2007). Although both pollen and leaf waxes are produced by plants, their production and dispersal have limited functional connection in the plant and they are expected to have different (but uncertain) source integration characteristics across vegetated areas, which may vary both with plant type and climate regime. Studies off West Africa have shown distal transport is possible (Schefuss et al., 2003), although local sources dominate (Dupont, 2011). Here, in the Gulf of Aden, pollen taxa confirm integration of varied local and distal sources, thought to include the south Ethiopian escarpment, the Afar triangle, and to a lesser extent the Horn of Africa, but perhaps not sites as far south as the Turkana Basin (Fig. 1).

In comparison, the $\delta^{13}\text{C}_{\text{pc}}$ values from East African Rift sites provide an indication of long-term trends within variable terrestrial landscapes within the rift valley, with regional climatic influences as well as local tectonic controls (Levin et al., 2011; Trauth et al., 2007). As pedogenic carbonates may form over 10^3 – 10^5 yr, $\delta^{13}\text{C}_{\text{pc}}$ values do not capture the short-term variability and environmental extremes that may be recorded in the pollen and $\delta^{13}\text{C}_{\text{wax}}$ records. However, the long-term vegetation trend in the Pliocene and Pleistocene is common to both the marine archive and the floodplain and lake-margin soils of the East African Rift system (Fig. 2).

Miocene and Pliocene–Pleistocene C_4 Expansions

The long perspective afforded by the extended records allows us to constrain the nature of the Miocene C_4 expansion in direct comparison with the later Pliocene–Pleistocene expansions. The 12 m.y. leaf wax carbon isotope record suggests that the Miocene C_4 expansion was achieved in two directional shifts occurring 11–9 Ma and 6–5 Ma, separated by a period of apparent stability. On land, peak values for the Late Miocene are recorded at 5.72 Ma ($\delta^{13}\text{C}_{\text{pc}} = -1.3\text{‰}$) in the Lothagam Formation in Turkana (Cerling et al., 2003), and at 4.4 Ma in the Sagantole Formation (-0.4‰) in the Middle Awash study area of the Afar region (WoldeGabriel

et al., 2009; Fig. 2). In the marine core, $\delta^{13}\text{C}_{\text{wax}}$ values are high across 5.8–4.4 Ma, with a single point defining a peak (-23.9‰) at 4.9 Ma. These data show that during the Late Miocene, C_4 vegetation in northeast Africa reached proportions almost as great as the later peak at 1.4 Ma, but there was a return to some of the lowest $\delta^{13}\text{C}_{\text{wax}}$ values reported (negligible C_4 proportions) by 4.3 Ma. Similar patterns are seen on land where there is a shift to more negative $\delta^{13}\text{C}_{\text{pc}}$ values in both the Awash and Turkana Basins after 4.4 Ma (Cerling et al., 2011). However, despite the return to late Middle Miocene $\delta^{13}\text{C}$ values, grass biomass and woody cover proportions are very different with only 10%–30% grass pollen in the earliest Pliocene versus 20%–50% grass pollen in the Middle Miocene, indicating dramatically different ecosystems. We find that C_3 grasslands and woodlands in the Miocene were replaced by a mix of C_4 grassland, C_3/C_4 shrubland, and woodland in the Pliocene. Overall, the Miocene and Pliocene trend was toward a reduction of grass pollen (presumably indicating a contraction of grasslands or a decline in grassland productivity) at the same time that C_4 grasses increased as a proportion of biomass ($\delta^{13}\text{C}$ positive shift).

In the Pliocene and Pleistocene, a consistent trend of positive shifts in both $\delta^{13}\text{C}_{\text{wax}}$ and $\delta^{13}\text{C}_{\text{pc}}$ values and decline in the proportion of grass pollen begins after 4.3 Ma (Fig. 2). The C_4 expansion across 4.3–1.4 Ma was of equal magnitude to the Miocene expansion, but the nature of the Pliocene–Pleistocene expansion was very different with progressive C_4 biomass increases across numerous 10^4 – 10^5 yr cycles, corroborating the variability that was previously reported (Feakins et al., 2005). These cycles in $\delta^{13}\text{C}_{\text{wax}}$ values are presumed to be obliquity- and precession-paced based on analysis of dust percentages in cores with continuous recovery collected around Africa (deMenocal, 1995). During this time a long-term reduction in the proportion of grass pollen suggests that absolute grassland productivity may have decreased or that grasslands in general declined relative to other habitats such as xeric shrubland (marked by abundant Amaranthaceae taxa), presumably related to increased aridity. These broad trends align with the progressive expansion of Northern Hemisphere glaciations after 2.7 Ma (Lisiecki and Raymo, 2005), supporting a role for the high latitudes in driving the tropical vegetation changes during the Pleistocene (Dupont, 2011; Schefuss et al., 2011). However, local insolation forcing (precession dominated) has also been implicated in tropical African vegetation changes (Denison et al., 2005; Dupont, 2011). We here confirm our earlier report (Feakins et al., 2005) that northeast African environmental variability began well before the onset of Northern Hemisphere glaciations, as early as 4.3 Ma.

CONCLUSIONS

This study synthesizes $\delta^{13}\text{C}_{\text{wax}}$, $\delta^{13}\text{C}_{\text{pc}}$, and pollen evidence to provide new insights into northeast African vegetation change during the past 12 m.y. Our enhanced $\delta^{13}\text{C}_{\text{wax}}$ record reveals that the regional C_4 biomass expansion between 11 and 5 Ma (Late Miocene) was reversed by 4.3 Ma and then followed by an equally large C_4 expansion from 4.3 to 1.4 Ma (Pliocene–Pleistocene). The combination of $\delta^{13}\text{C}$ and pollen data yields insights that neither the isotope nor pollen records could achieve alone. Firstly, extensive and/or productive Middle Miocene grasslands must have been C_3 dominated. Secondly, C_4 biomass increased substantially by ca. 9 Ma although grasslands were reduced in overall extent or productivity. Thirdly, the nature of the two C_4 -biomass expansions differed: the Miocene expansion occurred amidst extensive C_3 grasslands, whereas the Pliocene–Pleistocene C_4 expansion occurred in a context of reduced grasslands. Consistencies between $\delta^{13}\text{C}_{\text{wax}}$ and $\delta^{13}\text{C}_{\text{tooth}}$ in the Late Miocene and $\delta^{13}\text{C}_{\text{wax}}$ and $\delta^{13}\text{C}_{\text{pc}}$ in the Pliocene and Pleistocene give confidence that these are robust features of both the East African Rift and the wider northeast African environment.

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