Human impacts, climate change, and aquatic ecosystem response during the past 2000 yr at Lake Wandakara, Uganda

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ABSTRACT

Analyses of carbon and hydrogen isotope ratios of terrestrial leaf waxes and the carbon and nitrogen abundance, ratio, and isotopic composition of bulk sediments from Lake Wandakara, a crater lake in western Uganda, East Africa, document human and climatic controls on the aquatic system and on the surrounding terrestrial vegetation during the past two millennia. Our data indicate that Wandakara was a relatively stable, productive lake surrounded by C_3 vegetation from AD 70 to 1000. Abrupt changes in the $\delta^{13}C$ of terrestrial leaf waxes indicate a series of abrupt shifts in the relative abundance of C_3 and C_4 vegetation caused by a combination of climate change and human activities around Wandakara beginning at AD 1000. Abrupt shifts in bulk sediment organic geochemistry, particularly C/N ratios and $\delta^{15}N$, indicate that human activities at this time caused permanent changes in the limnology of Lake Wandakara, including eutrophication. Our results suggest that the biogeochemistry of Lake Wandakara was more sensitive to shifting human impacts than to climate variations during the past millennium, highlighting the importance of understanding the intensity of pre-colonial human impacts on Africa's aquatic ecosystems.

Introduction

Unraveling the causes of paleoenvironmental change is crucial to understanding the sensitivity and resilience of terrestrial and aquatic ecosystems to disturbance, as well as the complex interactions between climate, environment, and society. East African climate has fluctuated dramatically during the past two millennia, with major regional climate events registered by paleolimnological records at about AD 100, 1000, 1250, 1600 and 1800 (Verschuren et al., 2000; Alin and Cohen, 2003; Russell and Johnson, 2005, 2007). These events had an enormous impact on Africa's landscapes and lakes, including replacement of forests with grasslands during intervals of drought (Marchant and Taylor, 1998; Lamb et al., 2003), and changes in the productivity of East Africa's great lakes (e.g., Cohen et al., 2006). However, understanding the impacts of tropical African climate change must take into account large-scale use of the landscape by pre-colonial societies (Hamilton, 1972; Robertshaw et al., 2004). Complicating this issue, climate variations appear to have influenced cultural and political change in pre-colonial East African societies (Taylor, 1993; Taylor et al., 2000; Robertshaw et al., 2004), causing synergistic effects on African paleoenvironments.

A variety of factors obscure our view of the relative impacts of climate and humans on African ecosystems. First, African climate change exhibits significant regional variability (Verschuren, 2004; Russell et al., 2007; Russell and Johnson, 2007). Climate between AD 1450 and 1750, for instance, was characterized by wet conditions in easternmost Africa (Verschuren et al., 2000; Stager et al., 2005) and drought in the western rift valley in Uganda, Tanzania, and Malawi (Russell and Johnson, 2007). Such geographic gradients invalidate the assumption that paleoclimate records can be geographically extrapolated to infer climate impacts on local ecosystems. Second, many paleoclimate reconstructions from tropical Africa are based upon biogeochemical and paleoecological analyses of lake sediments and/or palynological reconstructions of vegetation (e.g., Bonnefille and Chalié, 2000; Talbot et al., 2006). These data provide the fundamental framework for our understanding of African climate history, yet both lake biogeochemistry and terrestrial vegetation are obviously sensitive to both climate and human impacts. Characterizing the complex and interactive impacts of paleoclimatic and socio-political change thus requires multiproxy methods, including proxies exclusively sensitive to climate.

Here we apply novel, compound-specific stable isotope indicators to investigate the impacts of climate change and human land clearance on terrestrial vegetation and lacustrine biogeochemistry during the past two millennia at Lake Wandakara, a small crater lake in western Uganda (Fig. 1). This is an ideal site at which to conduct this research because the century-scale climate history of western Uganda during the past two millennia has been well characterized by investigations of

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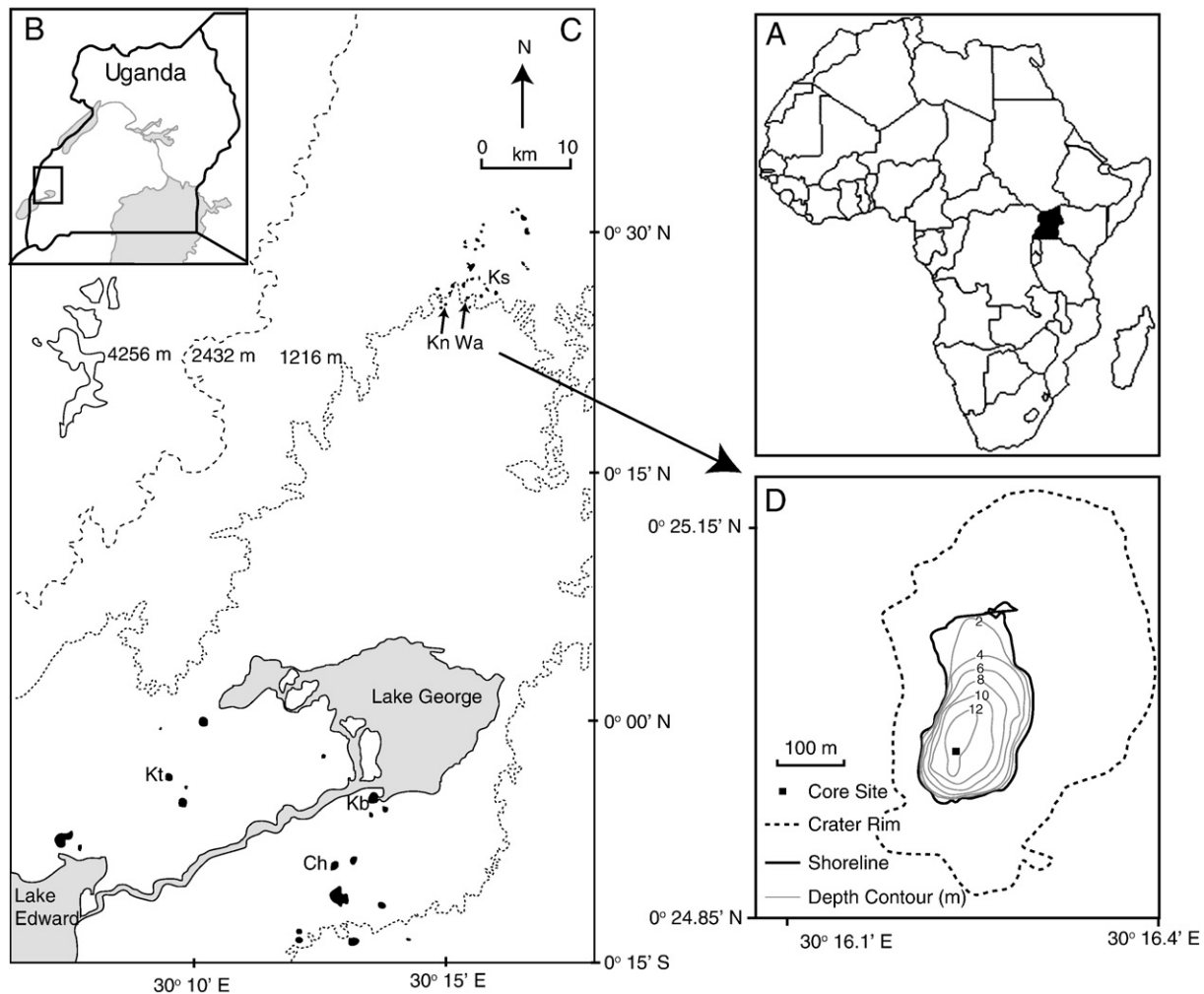E-mail address: James_Russell@Brown.edu (J.M. Russell).

Figure 1. (A) Map of Africa with Uganda shaded. (B) Map of Uganda. The inset square inset highlights the location of the study area. (C) The crater lake district of western Uganda, modified from Melack (1978). Initials correspond to the names of lakes that have been investigated for paleoclimate studies by Bessems et al. (2008). Ks is Kasenda, Kn is Kanyamukali, Wa is Wandakara, Kt is Kitagata, Kb is Kibengo, and Ch is Chibwera. (D) Bathymetric map of Lake Wandakara with our core site.

multiple crater lakes in the region (Bessems, 2007; Bessems et al., 2008; Russell et al., 2007), as well as Lake Edward (Russell and Johnson, 2007), providing a local climate history to guide the interpretation of past ecosystem changes. Second, archaeological studies have documented substantial human interactions with the landscape in western Uganda during the past 1000 yr (Robertshaw et al., 2004; Taylor et al., 2000). Indeed, palynological investigations of Lake Wandakara indicate major changes in local vegetation in response to both climate change and pre-colonial human activities (Ssemmanda et al., 2005). Our multiproxy approach builds upon these previous studies by demonstrating that pre-colonial human landscape clearance caused substantial changes in the biogeochemistry of Lake Wandakara, and provides a new method for investigating climatic versus anthropogenic impacts on vegetation and limnological processes.

Study site

Lake Wandakara is a maar crater lake located in the Kasenda lake district of western Uganda, in the western branch of the East African rift system (Fig. 1). The lake lies within a topographically closed basin within the larger catchment area of Lake Edward to the south. It is located 1170 m above sea level, has a surface area of 4 ha, and a maximum depth of 12.25 m. The water column is seasonally stratified, with an anoxic hypolimnion, and is slightly saline with a surface conductivity of ~1060 μS/cm and a pH of 8.9. The regional climate is

tropical sub-humid, with two distinct rainy seasons from March to May and from October to December (Nicholson, 1996). The annual average rainfall in western Uganda is 1300 mm, while the average annual evaporation is 1750 mm (Russell and Johnson, 2006). The lake's catchment is underlain by volcanic ash and basic volcanic rocks which have weathered to fertile soil (Bishop, 1965). This climate and soil naturally supports moist semi-deciduous forest (White, 1983); following human land clearance, however, crops such as maize, cassava, and banana are now farmed on Lake Wandakara's crater slopes.

Materials and methods

Sediment cores were taken in January 2001 and 2002 from the central, deepest part of Lake Wandakara using a single-drive piston corer for sub-recent sediments and a square-rod piston corer for deeper deposits. The topmost section containing unconsolidated sediment was sectioned upright in the field in 1-cm increments into Whirl-Pak bags to preserve physical and geochemical properties for dating. Deeper sediments were recovered in a stainless steel barrel using the square-rod piston corer, extruded in 1-m sections on site into a polyethylene sheath, and sealed in a PVC tube for transport. Multiple cores were taken to ensure overlap between adjacent core sections. Cores were shipped to Ghent University, Belgium, where they were split, macroscopically and microscopically described, and

sampled. The 4.81-m composite core sequence recovered from Lake Wandakara consists of massive to laminated silty clays with variable calcium carbonate and organic matter concentrations; detailed lithostratigraphic information is contained in Bessems (2007).

Core chronology for late Holocene deposits was determined using ^{137}Cs, ^{210}Pb, and ^{14}C dating. ^{137}Cs activities were measured by gamma spectroscopy at Queen's University, Kingston, Canada, while ^{210}Pb activity was constrained by alpha spectrometric measurement of radiation emitted from ^{210}Po at the University of Manitoba, Winnipeg, Canada. Radiometric ages were calculated using the constant rate of supply (CRS) ^{210}Pb dating model (Appleby and Oldfield, 1978). Chronology of pre-20th century deposits was determined based on accelerator mass spectrometry (AMS) radiocarbon dates of plant macrofossils and bulk organic mud (Table 1). Our age model also includes two ^{14}C dates on terrestrial plant macrofossils from the core studied by Ssemmanda et al. (2005), which we transferred to our cores through cross-correlation of loss-on-ignition profiles and visual lithostratigraphic markers, including sediment laminations.

Samples of 0.5-mL volume were taken every 4 cm for analyses of the total organic carbon and nitrogen abundance, ratio, and isotopic composition (%OC, %N, C/N, $\delta^{13}C_{org}$ and $\delta^{15}N_{org}$). Samples were soaked in 10% HCl for 1 h to remove carbonates, followed by rinses in high-purity distilled water to remove HCl. Treated samples were freeze-dried, ground with a mortar and pestle, and analyzed using a Carlo Erba Elemental Analyzer interfaced to a Finnigan Delta Plus XL isotope-ratio mass spectrometer through a Conflo II interface. Analytical precision on internal standards was 0.3‰ for $\delta^{15}N_{org}$ and 0.07‰ for $\delta^{13}C_{org}$. All results are reported relative to air for $\delta^{15}N_{org}$ and to VPDB for $\delta^{13}C_{org}$.

We measured the hydrogen and carbon isotopic composition of leaf wax fatty acids from 27 samples taken at 10- to 20-cm intervals throughout the core. Sample preparation followed the protocol outlined by Huang et al. (2004). Briefly, sediment samples were freeze-dried and ground, and free lipids were extracted in 9:1 dichloromethane:methanol using a Dionex accelerated solvent extrac-tor. Fatty acids were isolated using solid phase extraction (Aminopro-pyl Bond Elute®) in a glass column (Russell and Werne, 2007), and were methylated using anhydrous 2% HCl in methanol. Fatty acid methyl esters were purified using silica gel column chromatography prior to isotopic analysis. Ester-bound lipids were extracted from 15 of the sediment residues using saponification under reflux with 0.5 N KOH/MeOH with 2–3% water. The solution was acidified, and lipids were extracted with hexane. We then isolated, methylated, and purified the bound fatty acids using the procedure described above.

Compound identification and quantification were carried out using a gas chromatography (GC) flame ionization detector and GC–mass

spectrometry prior to isotopic analysis. An HP 6890 GC–pyrolysis system stable isotope spectrometer with a high-temperature pyrolysis reactor was used for hydrogen isotopic analysis of long-chain (C_{22} and higher) free and short-chain (C_{16} and C_{18}) bound fatty acid methyl esters (FAMES). Due to variable concentrations for different fatty acids, isotope measurements focused on only two long-chain waxes, C_{28} and C_{30} n-acid. Carbon isotopic analyses of long-chain FAMES were performed on an HP 6890 GC with a Combustion Interface interfaced to a Finnigan Delta$^+$ XL. The precision (1-sigma) of triplicate δD measurements was ≤ 2‰; precision on $\delta^{13}C$ analysis was ≤ 0.5‰. Accuracy was checked by analysis of laboratory isotopic standards between every six injections. All δD measure-ments are reported in per mil (‰) notation relative to SMOW, and $\delta^{13}C$ analyses are reported in ‰ notation relative to VPDB. Values were corrected for the isotopic composition of the added methyl group by mathematically removing their isotopic contributions (Huang et al., 2004).

Results and interpretations

Our multiproxy reconstruction of environmental change at Lake Wandakara is based primarily upon five different geochemical analyses of its sedimentary organic matter: C/N, the $\delta^{13}C$ and $\delta^{15}N$ of bulk organic matter, and the $\delta^{13}C$ and δD of fatty acids. Below we briefly summarize the primary controls on each of these and discuss their interpretation in the context of our record from Lake Wandakara.

Core chronology

The sediment core spans the interval from about AD 70 to 2000 (Fig. 2). ^{137}Cs activity has a maximum value at 33-cm depth (Fig. 2A), similar to the depth recorded by Ssemmanda et al. (2005), that probably records the 1963/64 fallout maximum. Total ^{210}Pb activity shows a fairly regular and exponential decline from values of 0.94 Bq/g at the core top to a supported value of 0.15 Bq/g at 96.5-cm depth (Fig. 2B). CRS age modeling indicates an average sedimentation rate of 0.060 ± 0.021 g/cm^2/yr in the ^{210}Pb-dated interval, with an age estimate of AD 1860 for 96.5-cm depth. Paired dating of terrestrial macrofossils and bulk organic matter indicates that a substantial radiocarbon reservoir exists in Lake Wandakara. We have applied a reservoir correction of 1865 ^{14}C yr to bulk ages based upon the average age differences between paired dates across the entire core (Bessems, 2007). Four of our eleven ^{14}C dated intervals returned outlying ages that may result from either sediment reworking or incorrect assump-tions regarding our reservoir correction. However, 4 dates from terrestrial macrofossils and 3 reservoir-corrected bulk organic carbon

Table 1
AMS ^{14}C from Lake Wandakara.

Depth (cm)	Lab no.	Dated material	^{14}C age ± error (yr AD)	Calibrated age (AD)	Calibrated age range (AD)
104.5	Poz-18552	OM	1655 ± 30	–	–
171	Poz-16552	OM	2150 ± 30	1548	1494–1601 (0.632)
253	Poz-16553	OM	2545 ± 35	1329	1267–1391 (1.0)
271	*Poz-18553*	*OM*	*2910 ± 35*	*986*	*938–1033 (0.877)*
351	*Poz-18629*	*OM*	*3585 ± 35*	*323*	*242–403 (1.0)*
392	Poz-5497	OM	3380 ± 35	561	502–620 (0.762)
446	Poz-19323	Leaf/stem	1740 ± 40	346	212–409 (0.988)
446	*Poz-18554*	*OM*	*2800 ± 35*	*1099*	*1022–1076 (1.0)*
462	Poz-19327	Leaf/stem	1790 ± 35	198	130–266 (0.744)
462	Poz-19325	Stem	1790 ± 35	198	130–266 (0.744)
462	Poz-19324	Leaf	1820 ± 35	190	120–259 (0.922)
462	*Poz-18578*	*OM*	*3320 ± 30*	*604*	*558–649 (0.988)*
234*	AAR-6885	Leaf	655 ± 40	1336	1276–1397 (1.0)

Samples marked by an asterisk are from Ssemmanda et al. (2005). Dated material includes organic matter (OM) and terrestrial plant leaves, stems, and twigs. Calibrated ages were obtained from Reimer et al. (2004) and Stuiver et al. (1998) after applying an 1865-yr reservoir correction to bulk organic matter dates. Calibrated age ranges are the highest probability range in the 2-sigma range, probabilities are given in parenthesis. The sample at 104.5-cm depth returned a negative range, indicating that the reservoir correction was likely too large for this sample. Samples in italic font were not included in our age model (Fig. 2) as they appeared as stratigraphic outliers.
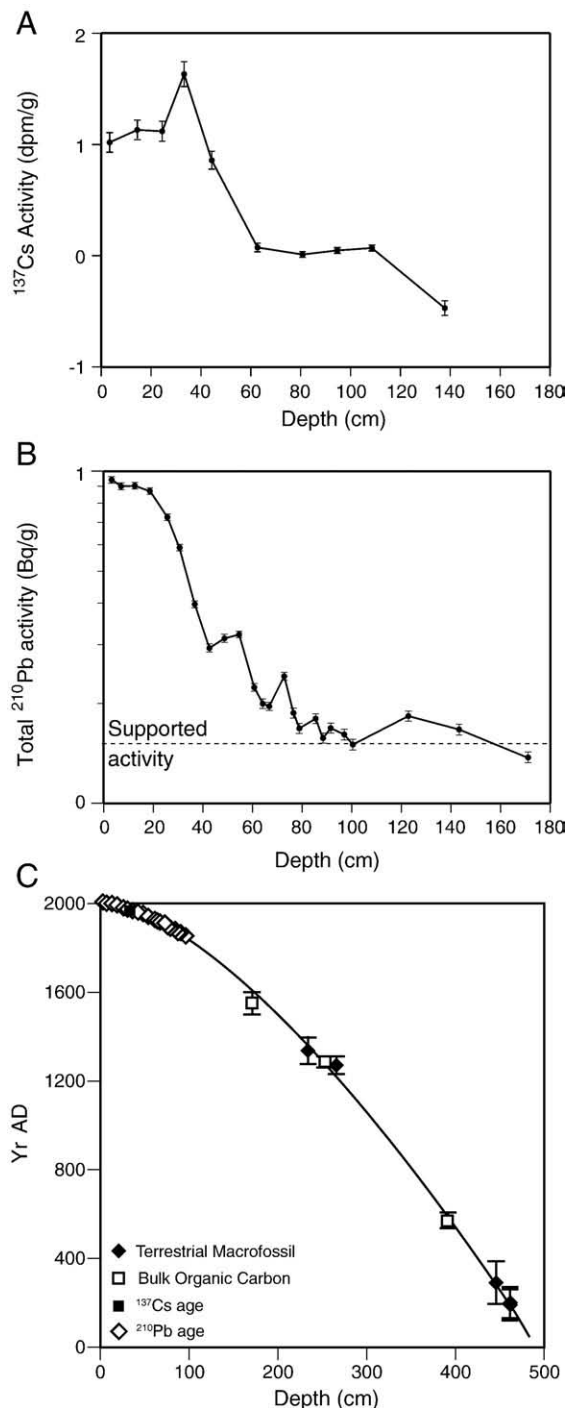
Figure 2. Year/depth model for Lake Wandakara based upon ^{137}Cs, ^{210}Pb, and AMS ^{14}C ages. The line represents a 3rd-order polynomial regression through dated intervals. [14]C dates on bulk organic carbon have been corrected for an 1865-yr reservoir effect. Four bulk ^{14}C dates that appeared to be stratigraphic outliers are not shown. Error bars indicate 2-sigma age ranges from Calib 5.0.2 (Reimer et al., 2004; Stuiver et al., 1998).

[14]C dated levels fit reasonably well with our ^{210}Pb and ^{137}Cs based age models. A 3rd-order polynomial regression to these data forms the basis for our age model (Fig. 2C). Results below are reported in years AD.

C/N: organic matter sources in Lake Wandakara

Organic carbon concentrations (on a carbonate-free basis) vary between 4.7 and 48.7%, while %N varies between 0.5 and 5.6% (Fig. 3).

%OC and %N values vary substantially at centennial time-scales around mean values of about 30% (%OC) and 3% (%N) until a dramatic decline centered on AD 1700. This time interval is represented by an ~35-cm-thick silt bed in our core, which Ssemmanda et al. (2005) show to have high magnetic susceptibility. In general, low %OC values reflect high siliciclastic mineral concentrations (Bessems, 2007). Following this minimum, %OC and %N return to their average values at about AD 1800.

The ratio of carbon to nitrogen has long been used to distinguish organic matter (OM) derived from phytoplankton and OM produced by terrestrial plants (Meyers, 1994; Prahl et al., 1980). Atomic C/N ratios of less than 10 are typically interpreted to reflect OM derived from phytoplankton, while C/N values greater than 20 reflect OM sourced from terrestrial plants (Talbot and Lærdal, 2000). However, selective loss of N from sedimentary organic matter during early diagenesis, as well as nitrogen limitation experienced by growing phytoplankton favor high sedimentary C/N ratios even when the OM is primarily of phytoplankton origin (Hecky et al., 1993; Talbot and Lærdal, 2000).

The C/N ratio of sedimentary OM in Lake Wandakara varies between 6.7 and 12.1 (Fig. 3), which is relatively low compared to many other East African lakes (Talbot and Lærdal, 2000). Given these low values combined with the effects of OM diagenesis and nitrogen limitation during phytoplankton growth, we interpret the C/N ratio to reflect predominantly aquatic sources of OM to the sediments in Lake Wandakara. In sediments deposited between AD 70 and 1250, the C/N of organic matter varies between 10.3 and 12.1, with a weakly rising trend and little coherent century-scale variability. These values likely represent aquatic biomass formed under relatively low N availability. The C/N ratio decreases abruptly from higher than 11 to less than 9 at AD 1250, then further declines from mean values of ~9 around AD 1400 to ~7.4 at the sediment surface, with little change in the low-organic silts deposited at about AD 1700. We interpret this decline to reflect changes in the stoichiometry of aquatic organic matter rather than a change in OM source, with the low C/N values of OM sourced predominantly from phytoplankton indicating progressively less N limitation for phytoplankton growth.

Carbon isotopes of bulk organic matter

There is a large range of possible $\delta^{13}C$ compositions of bulk sedimentary OM, due to variations in OM source, the degree of fractionation by terrestrial plants and aquatic algae, and processes that alter the isotopic composition of dissolved CO_2 in lakes. The photosynthetic pathway used by local vegetation is the dominant control on the $\delta^{13}C$ of terrestrial OM. Most plants, including trees, shrubs, and some grasses fix carbon through the C_3 pathway, and have bulk $\delta^{13}C$ values that typically lie between −30 and −25‰. In contrast, most tropical grasses as well as some crops such as maize, sugar cane, and millet, are C_4 vascular plants. C_4 plants have enriched $\delta^{13}C_{org}$ values relative to C_3, with typical values ranging from −16 to −10‰ (Meyers, 1997).

$\delta^{13}C_{org}$ in our core from Lake Wandakara averages −26.9‰ from AD 70 to 1150, with a weak positive trend towards the present (Fig. 3). From AD 1150 to present, $\delta^{13}C_{org}$ exhibits large, abrupt oscillations with peak values of −14.2‰, −13.9‰, and −15.7‰ at about AD 1300, 1450, and 1700, respectively. Intervening periods centered at AD 1400, 1550, and 1800 to the present have $\delta^{13}C_{org}$ values averaging −24‰, enriched relative to values in sediments deposited from AD 70 to 1150. The amplitude of the shifts beginning at AD 1250 is similar to the difference between end-member compositions of C_3 and C_4 plants, suggesting a control of vegetation type on $\delta^{13}C_{org}$; however, the low C/N of the sedimentary OM indicates that the dominant source of organic matter is aquatic, not terrestrial—including sediments deposited during the abrupt peaks in $\delta^{13}C_{org}$. Interestingly, much of the Wandakara sedimentary sequence falls well outside typical C/N-$\delta^{13}C_{org}$ compositional fields for freshwater algae and terrestrial plants

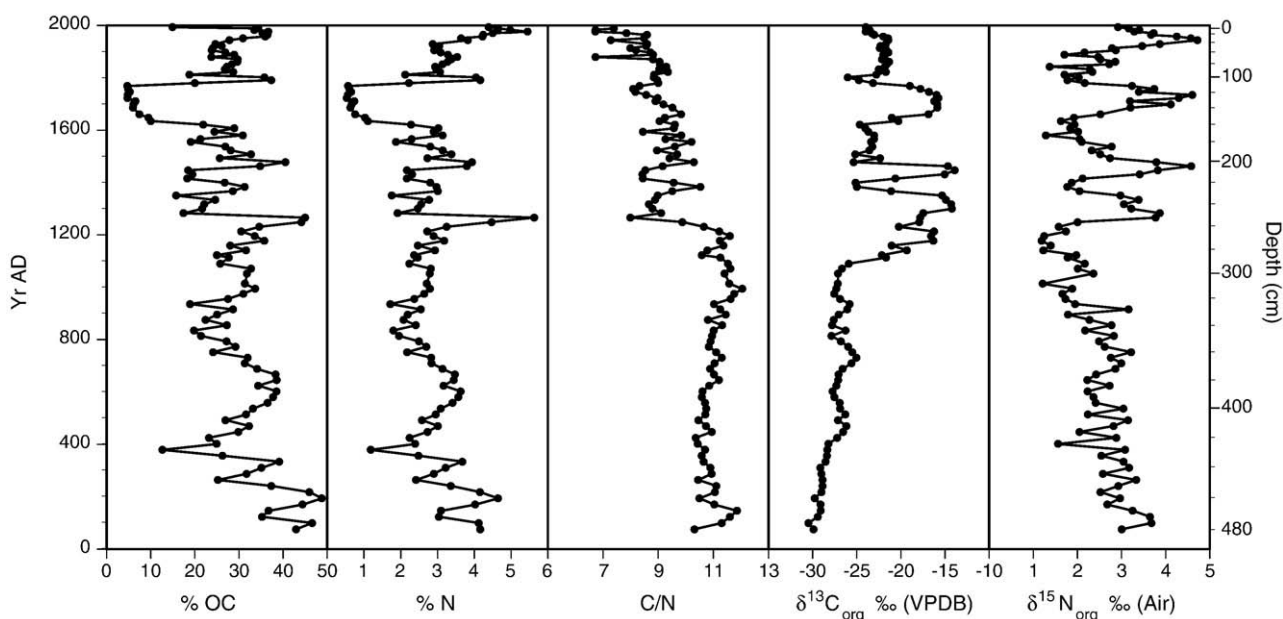**Figure 3.** Bulk organic geochemical measurements, including % organic carbon, % nitrogen, atomic C/N ratio, $\delta^{13}C_{org}$, and $\delta^{15}N_{org}$ from Lake Wandakara plotted by age (at left) and depth (at right). Note the non-linear depth scale, indicating compaction of sediment with depth.

(Fig. 4) (Meyers, 1994; Meyers and Ishiwarty, 1993). A variety of limnological processes, too numerous to review here, can enrich the $\delta^{13}C$ of aquatic OM, including bacterial processing of terrestrial C4 organic matter (Hedges et al., 1997), eutrophication (Schelske and Hodell, 1995), algal metabolism (Meyers, 1994; Talbot and Johannessen, 1992), and reservoir effects on DIC (Talbot, 1990). Additional proxies are thus needed to understand the $\delta^{13}C$ variability observed in Lake Wandakara through time.

Leaf wax carbon isotopes

Long-chain fatty acids from Lake Wandakara show strong even-over-odd chain-length predominance with peak abundances near the C_{30} *n*-acid, indicating that they are primarily derived from terrestrial plants (Eglinton and Hamilton, 1967). The $\delta^{13}C$ of leaf waxes is typically depleted relative to bulk biomass (Hedges et al., 1997), but C_3 and C_4 vegetation can still be distinguished because leaf waxes from C_3 plants typically have $\delta^{13}C$ values of about $-35‰$, while those from C_4 plants have values of about $-20‰$ (Huang et al., 2000). $\delta^{13}C$ values of the C_{28} and C_{30} *n*-acids in Lake Wandakara are strongly correlated (Fig. 5A); only trends in $\delta^{13}C$ for the C_{30} *n*-acid ($\delta^{13}C_{C30}$) will be described here. $\delta^{13}C_{C30}$ varies between -33 and $-28‰$ between AD 70 and 1100 with a weak positive trend toward the present (Fig. 5), reflecting an originally mostly C_3 terrestrial vegetation with gradually increasing C_4 abundances. $\delta^{13}C_{C30}$ shifts abruptly toward values of $\sim-20‰$ between AD 1200 and 1440 implying almost pure C_4 vegetation surrounding Lake Wandakara, then falls to $\sim-30‰$ around AD 1440. $\delta^{13}C_{C30}$ remains low until AD ~1600, then rises to a peak of $-20.1‰$ at AD 1740, declines to $-27‰$ by about AD 1800, and then varies between -26 and $-29.5‰$ from AD 1800 to the present. These more recent values reflect mixed C_3/C_4 vegetation, as exists in the crater basin today.

Abrupt shifts in the $\delta^{13}C_{C30}$ of Lake Wandakara sediments match both the timing and amplitude of abrupt changes in $\delta^{13}C_{org}$ (Fig. 6). It is highly unlikely that lake-driven variations in $\delta^{13}C_{org}$ would match the amplitude of vegetation-driven changes in $\delta^{13}C_{C30}$. We therefore argue that the $\delta^{13}C$ of bulk organic matter is largely controlled by shifts in the vegetation surrounding Lake Wandakara, despite a predominantly aquatic source of organic matter to the sediments as indicated by low C/N. Lakes receive large subsidies of organic carbon from their

watersheds, much of which is reprocessed by microbes before burial (Cole et al., 1994; Einsele et al., 2001; Meyers and Ishiwarty, 1993). This reprocessing can enrich the originally terrestrial organic matter with nitrogen while retaining the isotopic composition of terrestrial biomass (Hedges et al., 1997). Dissolved and particulate organic matter from soils bears the isotopic composition of terrestrial plants but has low C/N ratios relative to terrestrial plant OM (Meyers and Teranes, 2001), and therefore would require relatively little microbial alteration if soil OM is the predominant source of OM to lake sediments. Although the exact mechanisms are unclear, our $\delta^{13}C_{org}$ and $\delta^{13}C_{C30}$ data clearly show that vegetation type can exert a dominant control on the $\delta^{13}C$ of aquatic organic matter in tropical crater lakes. In addition, these data document large changes in the vegetation surrounding Lake Wandakara, confirming palynological evidence for substantial human and/or climatic impacts on vegetation in the region (Ssemmanda et al., 2005).
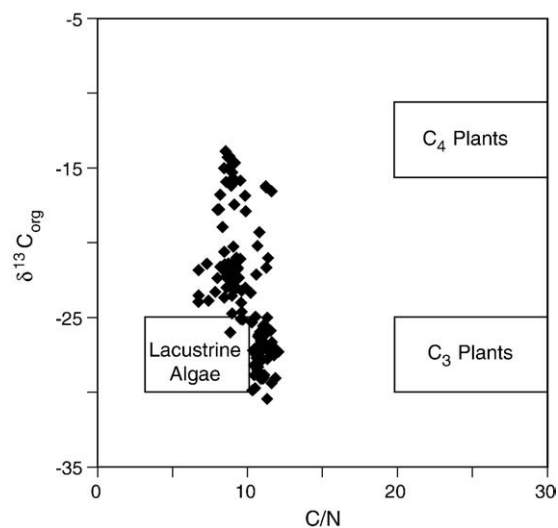

Figure 4. Crossplot of atomic C/N and $^{13}C_{org}$ values with typical compositions of lacustrine algae, C3 and C4 plants illustrated by boxes as suggested in Meyers (1997. Data from Lake Wandakara are indicated by diamonds, and do not appear consistent with typical algal or land plant compositions.
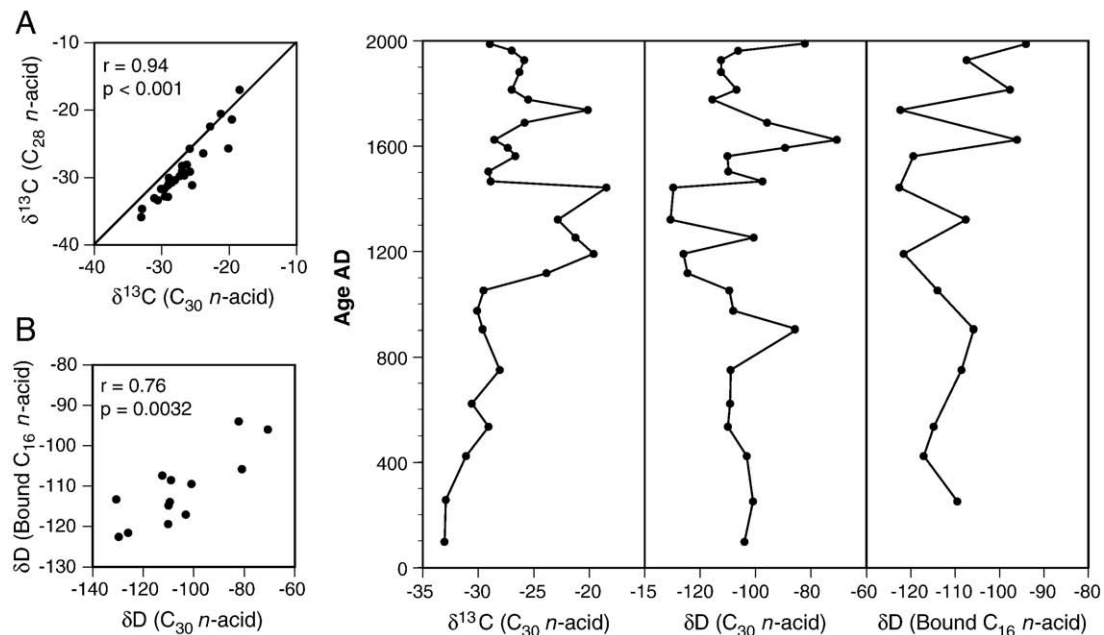
Figure 5. (A) Crossplot of $\delta^{13}CC30$ and $\delta^{13}CC28$ exhibiting strong correlation. (B) Crossplot of $\delta DC30$ and $\delta DC16$. At bottom, $\delta 13CC30$, $\delta DC30$, and $\delta DC16$ are plotted against age.

Fatty acid hydrogen isotopes

The δD of long-chain, terrestrially derived fatty acids is controlled by the δD of the water used by plants, transpiration from leaf surfaces, and kinetic fractionation during biosynthesis (Hou et al., 2008; Sessions et al., 1999). The δD of tropical rainfall, which forms the source water for leaf waxes, is controlled by the 'amount effect', which causes rainfall δD to become isotopically depleted as the rainfall amount increases (Dansgaard, 1964; Vuille et al., 2005). Decreased plant transpiration under more humid conditions will deplete the δD of leaf waters and the fatty acids formed from these waters, amplifying the amount effect, although growth chamber experiments have shown the transpiration effect to be relatively small (Hou et al., 2008). The amount effect and plant transpiration are typically interpreted to dominate leaf wax δD variations in tropical sediment records (e.g., Liu et al., 2005; Schefuß et al., 2005); however, vegetation type also can influence leaf wax δD through differences in D/H fractionation. C_4 and C_3 grasses appear to have broadly similar biosynthetic fractionation factors for D/H in leaf waxes (Chikaraishi and Naraoka, 2003), but field and culture experiments have shown that fatty acids produced by trees can have δD compositions enriched by ~50‰ relative to grasses from the same environment due to different apparent fractionation factors (Hou et al., 2007, 2008). However, recent surveys of long-chain fatty acids preserved in lake sediments in the American southwest have shown that interactions between humidity and vegetation type produce relatively invariant apparent fractionation between leaf wax and local rainfall δD (Hou et al., 2008). Although more arid conditions cause isotopically heavier rainfall and higher plant transpiration, increasing the δD of leaf waxes, drier environments also favor grasses, which produce isotopically depleted leaf waxes, balancing the amount and transpiration effects. Thus, although the first-order control on leaf wax δD in the tropics is the δD of meteoric waters, interactions between climate and vegetation suggest the potential for complex, non-linear responses of leaf wax δD to rainfall variability.

Considering these multiple controls on the δD of long-chain fatty acids, we also analyzed the δD of bound C_{16} fatty acid. Short-chain (C_{16}–C_{18}) fatty acids in lake sediments are derived primarily from aquatic sources (Eglinton and Hamilton, 1967; Huang et al., 2002), and

the principal control on their δD is the δD of lake water (Huang et al., 2002, 2004). The δD of closed-basin tropical lakes such as Wandakara reflects the hydrologic balance of the lake, with drier conditions causing isotopically enriched lake water due to both the amount effect on precipitation and kinetic fractionation during evaporation from the lake surface, which favors the retention of deuterium relative to hydrogen in the lake water (Craig, 1961). By comparing δD_{C16} and δD_{C30}, we can thus elucidate which δD variations reflect real hydroclimatic changes, as opposed to other processes.

δD_{C30} varies between -100 and $-110‰$ from AD 70 to 800, peaks at $-81‰$ around AD 950, then varies from -131 to $-124‰$ from AD 1100 to 1450 (aside from a single peak at AD 1250; Fig. 5). Over this interval, δD_{C16} rises from $-118‰$ to $107‰$ from AD 70 to 1000, then falls to values of $-120‰$ and lower from about AD 1200 to 1550, aside from a single peak at AD 1320. δD_{C30} rises from -130 to $-70‰$ between AD ~1450 and 1620, then falls to $-112‰$ by about 1760. δD_{C16} peaks at $-97‰$ at AD 1620, similar in timing to enrichments in δD_{C30}, then oscillates between values of -122 and $-96‰$ from AD 1700 to the present. δD_{C30} remains low from AD 1760 to 1920, then becomes more enriched toward the present. δD_{C16} and δD_{C30} are positively correlated (Fig. 5B), with intervals of isotopic enrichment centered on about AD 1000 and 1600, similar to the timing of major droughts in the region (Russell and Johnson, 2007).
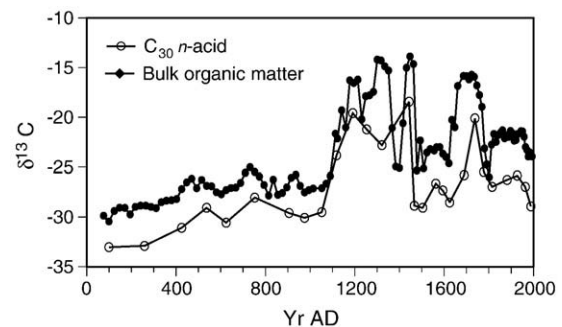

Figure 6. $\delta^{13}C$ of bulk organic matter and C_{30} n-acid plotted versus age. Note the similarity in both the timing and amplitudes of the observed changes.

If changes in vegetation surrounding Lake Wandakara were mainly driven by rainfall, $\delta^{13}C_{C30}$ and δD_{C30} should also be positively correlated: during intervals of drought shifts toward C_4 ecosystems would occur, recorded by enriched δD_{C30} values. However, $\delta^{13}C_{C30}$ and δD_{C30} are clearly negatively correlated (Fig. 5). In fact, large positive shifts in $\delta^{13}C_{C30}$ are associated with depleted δD_{C30} values, and peak $\delta^{13}C_{C30}$ from AD 1200 to 1440 occurs during an interval of regionally wet climate conditions (Russell et al., 2007, Russell and Johnson, 2007). This suggests that the abrupt shifts toward C_4 vegetation were not caused by climate but instead by human activities on the landscape, presumably forest clearance for agriculture (Ssemmanda et al., 2005).

Nitrogen isotopes of organic matter: biogeochemical impacts of forest clearance

Measured $\delta^{15}N$ values for East African vegetation range from 4 to 15‰, with no consistent differences in the $\delta^{15}N$ of trees and grasses (Muzuka, 1999). Conversion of organic matter to nitrate, which would be favored in oxic terrestrial soils, further enriches the $\delta^{15}N$ of nitrate that is transported to lakes (Meyers and Teranes, 2001). Algae typically discriminate against ^{15}N during assimilation (François et al., 1996; Talbot, 2001; Talbot and Lærdal, 2000), and the selective removal of ^{14}N during photosynthesis progressively enriches the residual nitrogen pool. Other processes that can enrich $\delta^{15}N_{org}$ include ammonia volatization (Collister and Hayes, 1991; Talbot and Johannessen, 1992), and microbial nitrification and denitrification (Talbot, 2001). On the other hand, nitrogen fixation by cyanobacteria produces OM with a $\delta^{15}N$ of ~0‰ (Talbot, 2001).

The shift in trends, variability, and values at about AD 1200 is also apparent in $\delta^{15}N_{org}$ (Fig. 5), indicating that human conversion of C_3- to C_4-dominated ecosystems surrounding Lake Wandakara strongly altered the lake's nitrogen cycle. $\delta^{15}N_{org}$ slowly declines from ~3‰ to ~1‰ from AD 400 to 1250. This shift likely indicates a gradual rise in the abundance of N-fixing cyanobacteria in the lake, perhaps related to decreasing N availability as suggested by increasing C/N (Hecky and Kling, 1987). After reaching a minimum value of 1.2‰ at AD 1170, $\delta^{15}N_{org}$ exhibits relatively large, 3‰ oscillations with enriched values at about AD 1300, 1460, 1730, and 1940. The switch in $\delta^{15}N_{org}$ variability is roughly coincident with changes in $\delta^{13}C_{org}$ and an abrupt decrease in C/N. We suggest that these variations result from an increased flux of isotopically enriched N from the landscape during conversion of forest to grassland. This hypothesis is confirmed by decreases in %OC during peaks in $\delta^{15}N_{org}$, implying dilution of %OC by clastic minerals. Interestingly, C/N values do not rise during periods of depleted $\delta^{13}C_{org}$ and $\delta^{15}N_{org}$ after AD 1250, suggesting that land clearance at that time resulted in a permanent switch toward elevated nitrogen concentrations in Lake Wandakara.

Discussion

Distinguishing human versus climatic controls on East African vegetation

Archaeological and palynological investigations provide evidence of human impact on western Ugandan landscapes beginning at about 500 BC with the arrival of Bantu people, who brought iron use and a range of different crops. Yet widespread forest clearance and environmental impacts are not suggested until about AD 1000, coincident with the appearance of large settlements, cereal agriculture, and new ceramic cultures. These populations then dispersed in the late 18th century to form pastoralist kingdoms (Robertshaw et al., 2004; Sutton, 1995, 1998; Taylor et al., 1999, 2000).

Palynological investigations of the vegetation history surrounding Lake Kasenda (~5 km from Wandakara) indicate replacement of forest by grassland by AD 1000, followed by a return to forest at both Kasenda and Wandakara at AD 1750 (Ssemmanda et al., 2005), in agreement with the documented regional human demographic changes. Yet forest clearance and regrowth at AD 1000 and 1800, respectively, in western Uganda must also have been affected by intervals of high rainfall and drought. Geochemical and stable isotopic investigations of sedimentary calcite in Lake Edward (Russell and Johnson, 2007) as well as lithostratigraphic studies of western Ugandan crater lakes (Russell et al., 2007) indicate a largely coherent hydroclimatic history for the region, with major droughts centered at about AD 100, 1100, and 1600, while AD 400, 1000, 1300, and the late 1700s were relatively wet. Geochemical data from Lake Edward indicates that the interval from AD 500 to 850 was also relatively dry (Russell and Johnson, 2005), although not all climate records in the region register changes during that time.

Because century-scale climate changes in East Africa appear linked to changes in large-scale atmospheric and oceanic circulation (Verschuren, 2004), it is highly unlikely that these climate events did not affect Lake Wandakara. Both carbonate geochemical (Bessems, 2007) and diatom-based salinity reconstructions from Lake Wandakara (Ryves et al., in revision) indicate drought conditions at ca. AD 1000 and 1600, coincident with the climate history outlined above. The effects of climate on Lake Wandakara can thus be inferred through comparison of our new data with this regional climate history.

Furthermore, we suggest that it may be possible to elucidate human versus climate impacts on vegetation using compound-specific stable isotopic data. Positive excursions in both δD_{C16} and δD_{C30} suggest drought conditions at about AD 1000 and 1600, identical in timing to major droughts during the past millennium identified at Lake Edward (Russell and Johnson, 2007). However, δD_{C30} exhibits an enormous range relative to δD_{C16}, with δD_{C30} values ranging from −70 to −130‰. The shift toward grassland at AD 1000 must therefore have influenced the δD_{C30} record due to biosynthetic fractionation differences between trees and grasses (Hou et al., 2007). Indeed, the enormous amplitude of shifts in δD_{C30} relative to δD_{C16} likely results from the replacement of forest with C_4 grasslands during wet periods—a process driven by humans rather than by climate. The amplified δD_{C30} response occurs because of a combination of the amount effect during wet periods and stronger isotopic fractionation by grasses relative to trees, both of which favor isotopically depleted δD_{C30} (Hou et al., 2008). This constitutes a novel method for detecting human impacts on vegetation, and highlights the importance of understanding the processes controlling vegetation changes when interpreting geochemical records of climate.

Human impacts on vegetation and aquatic ecosystems at Lake Wandakara

Paleolimnological investigations in tropical Africa have largely assumed that population densities prior to colonial times were too low to have significantly affected aquatic ecosystems. This contrasts with paleolimnological studies in Europe (Fritz, 1989; Renberg et al., 1993), South America (Binford et al., 1987; Abbott and Wolfe, 2003), and North America (Ekdahl et al., 2004) that document substantial prehistoric human impacts on lakes, including lake eutrophication, as well as palynological studies that indicate substantial human impacts on vegetation in East Africa (e.g., Taylor et al., 2000).

Our multiproxy dataset from Lake Wandakara, coupled with the regional paleoclimate reconstructions described above, allows us to distinguish both human impacts on vegetation as well as impacts on Lake Wandakara itself. From AD 70 until ~1000, Lake Wandakara was surrounded by C_3 vegetation. %OC, C/N and $\delta^{15}N_{org}$ data suggest a relatively productive aquatic ecosystem, with a gradually decreasing supply of dissolved N through time which perhaps resulted in increasing importance of cyanobacteria. δD_{C30} exhibits intermediate values during this interval, with a peak at AD 900 that may correlate with a minor drought, also registered by rising Mg/Ca in Lake Edward

(Fig. 7). Lake Wandakara thus appears to have been a relatively stable and resilient ecosystem during this time period, despite evidence for century-scale hydroclimatic change in western Uganda.

Lake Wandakara changed dramatically at AD 1000, when $\delta^{13}C$ data register an abrupt increase in the abundance of C_4 vegetation (Fig. 7). The $\delta^{13}C_{C30}$ signal could reflect either replacement of forest by C_4 grasses, or the local establishment of sorghum and millet farming, which have been documented in western Uganda at this time by archaeological studies (Sutton, 1995, 1998). Ssemmanda et al. (2005) interpreted grassland expansion at this time as "linked to human impact during a brief arid phase," and Taylor et al. (1999) present evidence for human forest clearance around AD 1000 at Kabata Swamp, ~10 km from Lake Wandakara. Regional paleoclimate records suggest dry conditions throughout equatorial East Africa beginning at about AD 1000 (Verschuren, 2004), yet δD_{C30} shifts towards relatively depleted values, indicating a strong control of vegetation type on δD. Although the relative importance of humans versus climate on grassland expansion at AD 1000 remains difficult to disentangle, we speculate that the negative shift in δD_{C30} despite drier conditions suggests that the primary factor influencing vegetation was humans, as climate effects typically dominate δD variability during climate-driven changes in vegetation (Hou et al., 2008).

Wet conditions returned to western Uganda from AD 1200 to 1450, yet C_4 vegetation persisted around Lake Wandakara, indicating strong human control of terrestrial vegetation. Interestingly, abrupt changes in C/N and $\delta^{15}N_{org}$ at Lake Wandakara do not occur until AD 1250, lagging changes in $\delta^{13}C_{org}$ by ~150 yr. This lag could reflect a delayed response of the lake to grassland expansion, the effects of increased rainfall during a period of intense human use of the landscape, or

increasing utilization of the Wandakara watershed by humans from AD 1250 on, resulting in the eutrophication of Lake Wandakara. In support of the latter interpretation, %OC and %N decline rapidly at AD 1250, indicating increases in clastic mineral input consistent with landscape clearance. These shifts are synchronous with increasing $\delta^{15}N_{org}$ but lag shifts in $\delta^{13}C_{org}$, likely indicating that climate-induced changes in terrestrial vegetation were followed by landscape clearance, siltation, and alteration of the nitrogen cycle at Lake Wandakara during the early part of the 2nd millennium AD. Robertshaw et al. (2004) argues for an increase in the number and size of agricultural settlements in western Uganda from AD 1180 to 1400, coincident with the timing of changes in the nitrogen cycle documented at Lake Wandakara. Moreover, western Ugandan farmers are thought to have fertilized agricultural fields with cattle manure, which would provide a source of isotopically enriched N to Lake Wandakara (Teranes and Bernasconi, 2000). In any case, that the abrupt changes in C/N and $\delta^{15}N_{org}$ do not occur until clear evidence appears for human alteration of the local vegetation indicates that Lake Wandakara was more sensitive to human activities than to climate variability at this time.

Dry conditions returned to western Uganda at AD 1450 and persisted until 1750 (Russell and Johnson, 2007). $\delta^{13}C_{C30}$ values average −27‰ during this interval, indicating that a mix of C_3 and C_4 vegetation surrounded Lake Wandakara, yet palynological data suggest dominance of grassland at this time (Ssemmanda et al., 2005). Abundant C_3 grasses seem unlikely given evidence for widespread drought. An alternative explanation could be the cultivation of C_3 crops in the Wandakara watershed at this time. A brief peak in $\delta^{13}C_{C30}$ indicates the re-expansion of C_4 grassland at AD 1750, coinciding with very low %OC (Fig. 2), reflecting heavy siltation in Lake Wandakara related to a second phase of watershed clearance. This is followed by the development of a mixed C_3/C_4 ecosystem, consistent with widespread evidence for the dispersal of human populations in western Uganda and associated forest regrowth. Despite evidence for reforestation around Lake Wandakara in the late 18th century, neither C/N ratios nor $\delta^{15}N_{org}$ return to the values observed in the 1st millennium AD. Human occupation of the basin in the 11th century thus caused semi-permanent changes in the chemistry of soils in the Wandakara basin and/or in the nitrogen biogeochemistry of Lake Wandakara.

Conclusions

We document profound historical changes in the aquatic ecosystem of Lake Wandakara, western Uganda, and the terrestrial vegetation within the lake's crater basin. Wandakara was a relatively stable, productive lake surrounded by C_3 vegetation prior to human alteration of the landscape about 1200 AD. Although the relative abundance of C_3 and C_4 vegetation around Wandakara varied between AD 1000 and today due to combinations of human activities and climate, human activities from about AD 1200 appear to have caused permanent changes in the limnology of Lake Wandakara, including eutrophication, suggesting that the biotgeochemistry of this lake is far more sensitive to human impacts than to climate. Whether Lake Wandakara is archetypical or atypical in this regard will require similar studies at other lakes in the region.
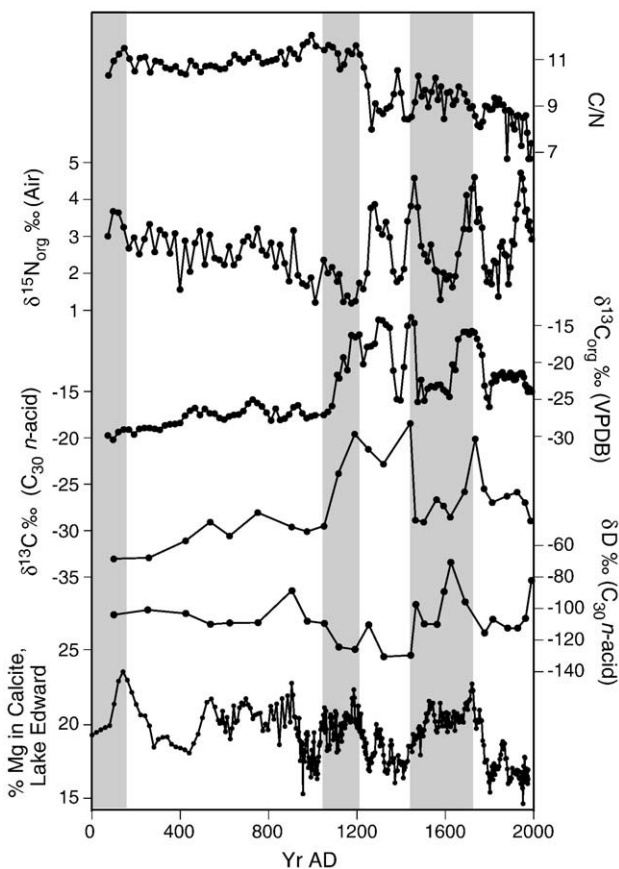
Acknowledgments

Figure 7. Key organic geochemical indicators from Lake Wandakara plotted with the % Mg in calcite from Lake Edward, an indicator of the salinity of the lake. Rising and high % Mg values in Lake Edward indicate more saline conditions and drought, while falling or low values indicate relatively wet conditions. Gray bars are droughts indicated by the Lake Edward record as well as other regional datasets discussed in the text.

References

Abbott, M.B., Wolfe, A.P., 2003. A 1300-year record of pre-Incan metallurgy recorded by lake sediments from the Bolivian Andes. Science.

Alin, S.R., Cohen, A.S., 2003. Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracode-inferred water-depth reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 199, 31–49.

Appleby, P.G., Oldfield, F., 1978. The calculation of ^{210}Pb dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. Cantena 5, 1–8.

Bessems, I., 2007. Late-Holocene climatic reconstruction in equatorial East Africa: sedimentology and stable isotope geochemistry of lake deposits. Universiteit Gent.

Bessems, I., Verschuren, D., Russell, J.M., Hus, J., Cumming, B., 2008. Paleolimnological evidence for widespread late-18th century drought across equatorial East Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 259, 107–120.

Binford, M.W., Brenner, M., Whitmore, T.J., Higuera-Gundy, A., Deevey, E.S., Leyden, B., 1987. Ecosystems, paleoecology, and human disturbance in subtropical and tropical America. Quaternary Science Reviews 6, 115–128.

Bishop, W.W., 1965. Quaternary geology and geomorphology in the Albertine Rift Valley, Uganda. Geologic Society of America Special Publication 48, 293–320.

Bonnefille, R., Chalié, F., 2000. Pollen-inferred precipitation time-series from equatorial mountains, Africa, the last 40 kyr BP. Global Planetary Change 26, 1257–1266.

Chikaraishi, Y., Naraoka, H., 2003. Compound-specific dD and d13C analyses of n-alkanes extracted from terrestrial and aquatic plants. Phytochemistry 63, 361–371.

Cohen, A.S., Lezzar, K.E., Cole, J., Dettman, D.L., Ellis, G.S., Eagle, M., Chorokoa, K., Plisnier, P.D., Langenberg, V., Michelo, V., Zilifi, D., 2006. Late Holocene linkages between decade-scale climate variability and productivity at Lake Tanganyika, Africa. Journal of Paleolimnology 36.

Cole, J.J., Caraco, N.F., Kling, G., Kratz, T.K., 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science 265, 1568–1570.

Collister, J.W., Hayes, J.M., 1991. A preliminary study of the carbon and nitrogen isotope biogeochemistry of lacustrine sedimentary rocks from the Green River Formation, Wyoming, Utah, and Colorado. U.S. Geological Survey Bulletin A–G, C1–C16.

Craig, H., 1961. Isotopic variation in meteoric waters. Science 133, 1702–1703.

Dansgaard, W., 1964. Stable isotopes in precipitation. Tellus 16, 436–468.

Eglinton, G., Hamilton, R.J., 1967. Leaf epicuticular waxes. Science 156, 1332–1334.

Einsele, G., Yan, J., Hinderer, M., 2001. Atmospheric carbon burial in modern lake basins and its significance for the global carbon budget. Global Planetary Change 30, 167–195.

Ekdahl, E., Teranes, J.L., Guilderson, T., Turton, C.L., McAndrews, J.H., Wittkop, C., Stoermer, E.F., 2004. Prehistorical record of cultural eutrophication from Crawford Lake, Canada. Geology 32, 745–748.

François, R., Pilskaln, C.H., Altabet, M., 1996. Seasonal variation in the nitrogen isotopic composition of sediment trap materials collected in Lake Malawi. In: Johnson, T.C., Odada, E.O. (Eds.), The Limnology, Climatology, and Paleoclimatology of the East African Lakes. Gordon and Breach, Amsterdam, pp. 241–250.

Fritz, S.C., 1989. Lake development and limnological response to prehistoric and historic land-use in Diss, Norfolk, U. K. Journal of Ecology 77, 182–202.

Hamilton, A.C., 1972. The interpretation of pollen diagrams from highland Uganda. Palaeoecology of Africa 7, 45–149.

Hecky, R.E., Kling, H.J., 1987. Phytoplankton ecology in the great lakes of the rift valleys of central Africa. Archiv fur Hydrobiologie Ergebnisse Limnologie 25, 3–34.

Hecky, R.E., Campbell, P., Hendzel, L.L., 1993. The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. Limnology and Oceanography 38, 1476–1481.

Hedges, J.I., Keil, R.G., Benner, R., 1997. What happens to terrestrial organic matter in the ocean? Organic Geochemistry 27, 195–212.

Hou, J., D'Andrea, W., MacDonald, D., Huang, Y., 2007. Hydrogen isotope variability in leaf waxes among terrestrial and aquatic plants around Blood Pond, Massachusetts (USA). Organic Geochemistry 38, 977–984.

Hou, J., D'Andrea, W., Huang, Y., 2008. Can sedimentary leaf waxes record D/H ratios of continental precipitation? Field, model, and experimental assessments. Geochimica et Cosmochimica Acta. 72, 3503–3517.

Huang, Y., Dupont, L., Sarnthein, M., Hayes, J.M., Eglinton, G., 2000. Mapping of C4 plant input from North West Africa into North East Atlantic sediments. Geochimica et Cosmochimica Acta 64, 3505–3513.

Huang, Y., Shuman, B., Wang, Y., Webb, T., 2002. Hydrogen isotope ratios of palmitic acid in lacustrine sediments record late-Quaternary climate variations. Geology 30, 1103–1106.

Huang, Y., Shuman, B., Wang, Y., Webb, T., 2004. Hydrogen isotope ratios of individual lipids in lake sediments as novel tracers of climatic and environmental change: a surface sediment test. Journal of Paleolimnology 31, 363–375.

Lamb, H.F., Derbyshire, I., Verschuren, D., 2003. Vegetation response to rainfall variation and human impact in central Kenya during the past 1100 years. Holocene 13, 285–292.

Liu, W., Huang, Y., An, Z., Clemens, S.C., Li, L., Prell, W.L., Ning, Y., 2005. Summer monsoon intensity controls C4/C3 plant abundance during the last 35 ka in the Chinese Loess Plateau: carbon isotope evidence from bulk organic matter and individual leaf waxes. Palaeogeography, Palaeoclimatology, Palaeoecology 220, 243–257.

Marchant, R., Taylor, D., 1998. Dynamics of montane forest in central Africa during the late Holocene: a pollen-based record from western Uganda. Holocene 8, 375–381.

Melack, J.M., 1978. Morphometric, physical, and chemical features of the volcanic crater lakes of Western Uganda. Archiv fur Hydrobiologie 85, 430–453.

Meyers, P.A., 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. Chemical Geology 144, 289–302.

Meyers, P.A., 1997. Organic geochemical proxies of paleoceanographic, paleolimnologic, and paleoclimatic processes. Organic Geochemistry 27, 213–250.

Meyers, P.A., Ishiwarty, R., 1993. Lacustrine organic geochemistry — an overview of indicators of organic matter sources and diagenesis in lake sediments. Organic Geochemistry 20, 867–900.

Meyers, P.A., Teranes, J.L., 2001. Sediment organic matter. In: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments. Kluwer Academic Publishers, Dordrecht.

Muzuka, A.N.N., 1999. Isotopic compositions of tropical East African flora and their potential as source indicators of organic matter in coastal marine sediments. Journal of African Earth Sciences 28, 757–766.

Nicholson, S.E., 1996. A review of climate dynamics and climate variability in Eastern Africa. In: Johnson, T.C., Odada, E.O. (Eds.), The Limnology, Climatology, and Paleoclimatology of the East African Lakes. Gordon and Breack Publishers, Amsterdamn, pp. 25–56.

Prahl, F.G., Bennett, J.T., Carpenter, R., 1980. The early diagenesis of aliphatic hydrocarbons and organic matter in sedimentary particulates from Dabob Bay, Washington. Geochimica et Cosmochimica Acta 44.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C., Blackwell, P.G., Buck, C.E., Burr, G.S., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T., Hogg, A.G., Hughen, K.A., Kromer, B., McCormac, F.G., Manning, S.W., Ramsey, C.B., Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J., Weyhenmeyer, C.E., 2004. IntCal04 terrestrial radiocarbon age calibration 26–0 ka BP. Radiocarbon 46, 1029–1058.

Renberg, I., Korsman, T., Birks, H.J.B., 1993. Prehistoric increases in the pH of acid sensitive Swedish lakes caused by land-use changes. Nature 362, 824–827.

Robertshaw, P., Taylor, D., Doyle, S., Marchant, R., 2004. Famine, climate, and crisis in Western Uganda. In: Battarbee, R.W., Gasse, F., Stickley, C.E. (Eds.), Past Climate Variability through Europe and Africa, Developments Palaeoenvironmental Research, Springer, Dordrecht, pp. 535–547.

Russell, J.M., Johnson, T.C., 2005. A high-resolution geochemical record from Lake Edward, Uganda-Congo, and the timing and causes of tropical African drought during the late Holocene. Quaternary Science Reviews 24, 1375–1389.

Russell, J.M., Johnson, T.C., 2006. The water balance and stable isotope hydrology of Lake Edward, Uganda-Congo. Journal of Great Lakes Research 32, 77–90.

Russell, J.M., Johnson, T.C., 2007. Little Ice Age drought in equatorial Africa: ITCZ migrations and ENSO variability. Geology 35, 21–24.

Russell, J.M., Werne, J.P., 2007. The use of solid phase extraction columns in fatty acid purification. Organic Geochemistry 38, 48–51.

Russell, J.M., Eggermont, H.E., Verschuren, D., 2007. Spatial complexity of Little Ice Age climate in East Africa: sedimentary records from two crater lake basins in Western Uganda. Holocene 17, 183–193.

Ryves, D.B., Mills, K., Bennike, O., Brodersen, K.P., Lamb, A.L., Leng, M.J., Russell, J.M., Ssemmanda, I., in revision. Testing the coherence of paired lakes to environmental change: a late Holocene multiproxy palaeolimnological study from two crater lakes in western Uganda. Quaternary Science Reviews.

Schefuß, E., Schouten, S., Schneider, R.R., 2005. Climatic controls on central African hydrology during the past 20,000 years. Nature 437, 1003–1006.

Schelske, C.L., Hodell, D.A., 1995. Using carbon isotopes of bulk sedimentary organic matter to reconstruct the history of nutrient loading and eutrophication in Lake Erie. Limnology and Oceanography 40, 918–929.

Sessions, A.L., Burgoyne, T.W., Schimmelmann, A., Hayes, J.M., 1999. Fractionation of hydrogen isotopes in lipid biosynthesis. Organic Geochemistry 30, 1193–1200.

Ssemmanda, I., Ryves, D.B., Bennike, O., Appleby, P.G., 2005. Vegetation history in western Uganda during the last 1200 years: a sediment-based reconstruction from two crater lakes. Holocene 15, 119–132.

Stager, J.C., Ryves, D.B., Cumming, B., Meeker, L., Beer, J., 2005. Solar variability and the levels of Lake Victoria, East Africa, during the last millennium. Journal of Paleolimnology 33, 243–251.

Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, F.G., van der Plicht, J., Spurk, M., 1998. INTCAL98 radiocarbon age calibration, 24,000–0 cal BP. Radiocarbon 40, 1041–1083.

Sutton, J.E.G., 1995. The growth of farming communities in Africa from the equator southwards. Azania 29 (/30), 1–332.

Sutton, J.E.G., 1998. Ntusi and Bigo: farmers, cattle-herders, and rulers in western Uganda, AD 1000–1500. Azania 33, 39–72.

Talbot, M.R., 2001. Nitrogen isotopes in paleolimnology. In: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change using Lake Sediments Volume 2: Physical and Geochemical Methods. Kluwer Academic Publishers, Dordrecht, pp. 401–440.

Talbot, M.R., 1990. A review of the paleohydrological interpretation of carbon and oxygen isotopic ratios in primary lacustrine carbonates. Chemical Geology (Isotope Geoscience Section) 80, 261–279.

Talbot, M.R., Johannessen, T., 1992. A high resolution paleoclimatic record for the last 27,500 years in tropical West Africa from the carbon and nitrogen isotopic composition of lacustrine organic matter. Earth Planetary Sciences Letter 110, 23–37.

Talbot, M.R., Lærdal, T., 2000. The late Pleistocene–Holocene paleolimnology of Lake Victoria, East Africa, based upon elemental and isotopic analyses of sedimentary organic matter. Journal of Paleolimnology 23, 141–164.

Talbot, M.R., Jensen, N.B., Laerdal, T., Filippi, M.L., 2006. Geochemical responses to a major transgression in giant African lakes. Journal of Paleolimnology 35, 467–489.

Taylor, D., 1993. Environmental change in montane southwest Uganda: a pollen record for the Holocene from Ahakagyezi Swamp. Holocene 3, 324–332.

Taylor, D., Marchant, R., Robertshaw, P., 1999. A sediment-based history of medium altitude forest in central Africa: a record from Kabata Swamp, Ndale volcanic field, Uganda. Journal of Ecology 87, 303–315.

Taylor, D., Robertshaw, P., Marchant, R., 2000. Environmental change and political upheaval in precolonial western Uganda. Holocene 10, 527–536.

Teranes, J.L., Bernasconi, S.M., 2000. The record of nitrate utilization and productivity limitation provided by $\delta^{15}N$ values in lake organic matter — a study of sediment trap and core sediments from Baldeggersee, Switzerland. Limnology and Oceanography 45, 801–813.

Verschuren, D., 2004. Decadal and century-scale climate variability in tropical Africa during the past 2,000 years. In: Battarbee, R.W. (Ed.), Past Climate Variability Through Europe and Africa. Elsevier Paleoenvironmental Research Book Series, Amsterdam.

Verschuren, D., Laird, K.R., Cumming, B., 2000. Rainfall and drought in equatorial East Africa during the past 1,100 years. Nature 403, 410–414.

Vuille, M., Werner, M., Bradley, R.S., Keimig, F., 2005. Stable isotopes in precipitation in the Asian monsoon region. Journal of Geophysical Research 110, 108.

White, F., 1983. The Vegetation of Africa. A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa. UNESCO, Paris.