Wet and arid phases in the southeast African tropics since the Last Glacial Maximum

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ABSTRACT

Plant leaf wax carbon isotopes provide a record of C_3 versus C_4 vegetation, a sensitive indicator of aridity, from the southeast African tropics since the Last Glacial Maximum. Wet and arid phases in southeast Africa were in phase with conditions in the global tropics from 23 to 11 ka, but at the start of the Holocene these relationships ended and an antiphase relationship prevailed. The abrupt switch from in phase to out of phase conditions may partially be attributed to a southward displacement of the Intertropical Convergence Zone (ITCZ) during the last glacial. Southward displacements of the ITCZ are also linked to arid conditions in southeast Africa during the Younger Dryas and the Little Ice Age.

Keywords: Africa, C_4 vegetation, Younger Dryas, Intertropical Convergence Zone.

INTRODUCTION

In tropical Africa, changes in the hydrological cycle have a far greater impact on human welfare than does the relatively small range of temperature variability. Thus it is important to understand the timing of past wet and arid phases in low-latitude regions. Tropical vegetation is a sensitive indicator of aridity because its distribution is mainly controlled by precipitation, which, in tropical East Africa, is influenced by the convective intensity and seasonal migrations of the Intertropical Convergence Zone (ITCZ) and the Inter-Oceanic Confluence (IOC) (Leroux, 2001). The C_3 (Calvin-Benson) and C_4 (Hatch-Slack) cycles are the two main pathways of carbon fixation utilized by plants (O'Leary, 1981). C_4 plants are characterized by higher water-use efficiency and are common today in tropical savannas, temperate grasslands, and semiarid regions (Raven et al., 1999). Aridity is the dominant control on the large-scale distribution of C_3 versus C_4 vegetation in tropical Africa (Schefuß et al., 2003), and thus changes in aridity can be examined by determining the past distribution of C_3 versus C_4 vegetation.

Lake Malawi (Fig. 1) sediments have provided one of the few continuous and high-resolution climate records since the Last Glacial Maximum (LGM) on the African continent. Aridity in Lake Malawi has been inferred from lake-level histories based on seismic reflection data (Johnson and Ng'ang'a, 1990), benthic diatom assemblages (Gasse et al., 2002), and geochemical analyses of endogenic calcite (Ricketts and Johnson, 1996). While the evidence for a major lake-level lowstand during the LGM is indisputable, the history of aridity in the region during the Holocene, particularly regarding conditions in the early Holocene, has not been resolved. Seismic reflectors are not well dated, the relative abundance of benthic diatoms can be influenced by preservation and sediment redeposition, and the presence and/or absence of endogenic carbonates in sediments is not a particularly sensitive indicator of hydrological conditions.

In comparison, tropical vegetation is a sensitive indicator of aridity, and the carbon isotopic composition of plant leaf waxes, used to distinguish between inputs of C_3 and C_4 vegetation (Collister et al., 1994), provides an additional independent method of examining past aridity.

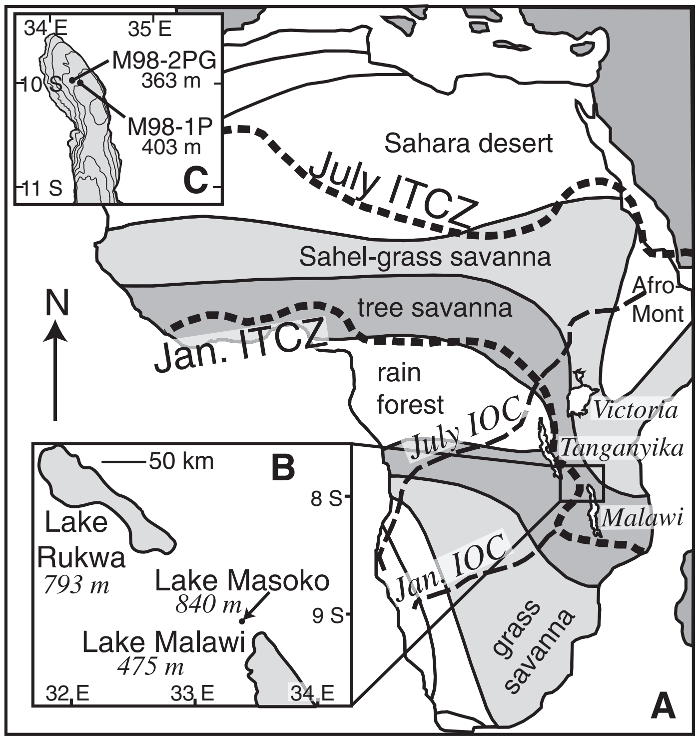

Figure 1. A: Vegetation zones of East Africa (Schefuß et al., 2003) and summer and winter positions of Intertropical Convergence Zone (ITCZ) and Inter-Oceanic Confluence (IOC) (Leroux, 2001). The IOC separates Atlantic and Indian Ocean moisture. B: Location of Lake Malawi (LM) in relation to Lakes Masoko and Rukwa. C: Location of sediment cores M98–1P (10°15.99′S, 34°19.19′E) and M98–2PG (9°58.6′S, 34°13.8′E) in the northern basin of LM.

Long-chain, odd-numbered *n*-alkanes (C_{25}-C_{35}) are a major component of terrestrial plant leaf waxes (Eglinton and Hamilton, 1967) and are generally well preserved in sediments. Lake Malawi is located near the present southernmost extent of the ITCZ and the lake's vast drainage basin is dominated by tree savanna (mainly C_3 plants), but grass savanna (mainly C_4 grasses) is present to both the north and south (Fig. 1). The proximity of Lake Malawi to this ecosystem boundary makes it a sensitive location to examine past aridity-driven vegetation shifts.

METHODS

We examined sediment cores M98–1P and M98–2PG from the north basin of Lake Malawi (Fig. 1). The age models of both cores were previously published (Johnson et al., 2002, 2001) and are not discussed further here. Ages are reported as thousands of calibrated years (cal ka) before present. Compound-specific carbon isotope analysis of *n*-alkanes was performed using gas chromatography–isotope ratio monitoring–mass spectrometry. Each *n*-alkane sample was run in duplicate and the standard deviation of all samples is <± 0.5‰. Method details are available in the GSA Data Repository.[1]

RESULTS AND DISCUSSION

Lake Malawi samples are characterized by a moderate to high odd versus even carbon number predominance (average carbon preference index of 3.9) indicating terrestrial plant inputs (Eglinton and Hamilton, 1967). We use the weighted mean $\delta^{13}C$ values of the C_{29}–C_{33} *n*-alkanes to examine past vegetation shifts and hereafter refer to this record as $\delta^{13}C_{alk}$. The percentage of C_4 grasses is estimated from a binary mixing model based on $\delta^{13}C_{alk}$, assuming end-member values of –36‰ and –21.5‰ for C_3 and C_4 vegetation, respectively (Collister et al., 1994; Fig. 2).

Lake Malawi $\delta^{13}C_{alk}$ values were enriched during the LGM, corresponding to an estimated vegetation assemblage of 61% C_4 grasses (Fig. 2B). Following the LGM, a gradual transition to increased C_3 abundances occurred until 13.6 ka. The onset of the Younger Dryas (YD) is marked by an abrupt return to increased C_4 inputs, and represents a shift from 45% to 60% C_4 grasses. Fluctuating but generally heavier $\delta^{13}C_{alk}$ values during the early Holocene (11–7.7 ka) indicate a vegetation assemblage of 49%–55% C_4 grasses. C_3 inputs increased after 7.7 ka, and C_3 vegetation reached maximum abundance at 4.9 ka. Subsequently, a return to increased C_4 abundances occurred; 56% C_4 grasses are noted at 0.4 ka.

Temperature, aridity, and the concentration of atmospheric carbon dioxide (pCO_2) can influence C_3 versus C_4 variability (Schefuß et al., 2003). Comparing the Lake Malawi $\delta^{13}C_{alk}$ record to the Taylor Dome CO_2 record (Monnin et al., 2001), we note that increased abundances of C_4 vegetation occur at times of low (LGM), intermediate (YD), and high (Holocene) pCO_2 (Fig. 2C), suggesting, as previously reported (e.g., Huang et al., 2001), that pCO_2 changes alone are insufficient to drive vegetation change. Comparing the $\delta^{13}C_{alk}$ record to the Lake Malawi temperature record (Powers et al., 2005), a correlation is noted between cooler temperatures and heavier $\delta^{13}C_{alk}$ values (Fig. 2B). While it may appear that temperature is the main control on vegetation type, we note that strong links between temperature and aridity exist in southeast Africa, with warm and wet and cool and dry conditions being associated (Powers et al., 2005; Brown and Johnson, 2005; Johnson et al., 2002). Furthermore, the observed relationship between $\delta^{13}C_{alk}$ and temperature, with increased C_4 abundances noted at times of cooler temperatures, contradicts previous studies that found increased abundances of C_4 grasses associated with warmer temperatures (Livingstone and Clayton, 1980;

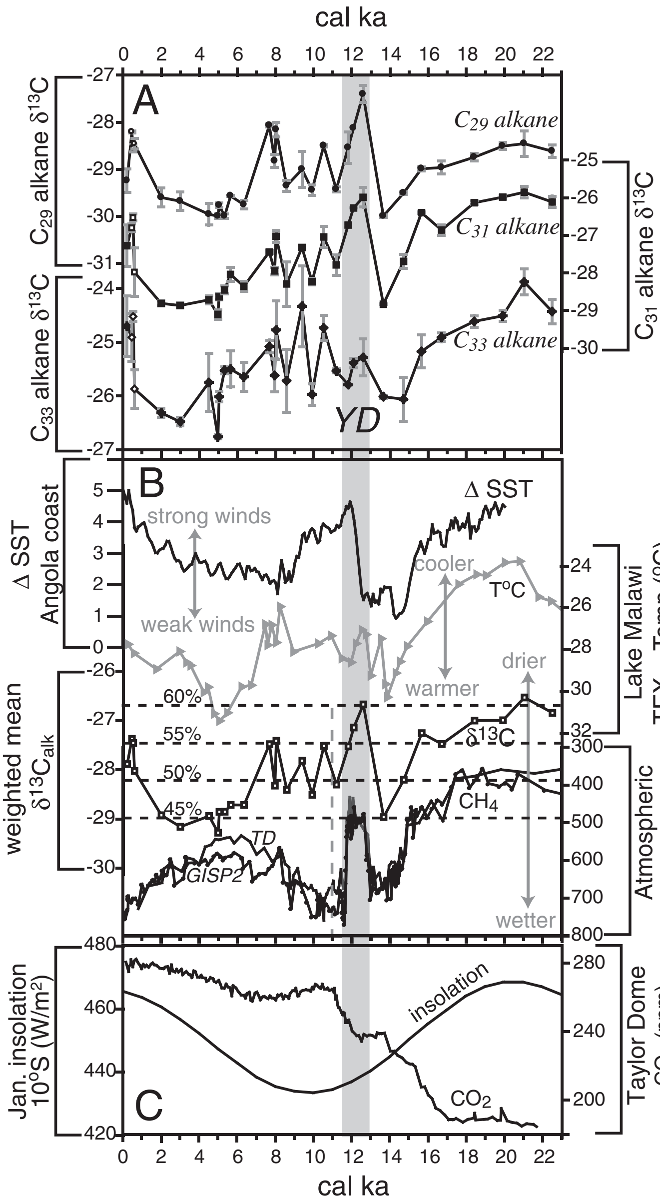

Figure 2. African paleoclimate records. Younger Dryas (YD) cold period is highlighted in all graphs. A: Carbon isotope composition of the C_{29}-C_{33} *n*-alkanes. Solid data points indicate samples from core M98–1P and open data points indicate samples from core M98–2PG. Error bars indicate the standard deviation of duplicate runs. B: Atmospheric methane (CH_4) records from the Greenland Ice Sheet Project (GISP2) and Taylor Dome (TD, Antarctica) ice cores (Brook et al., 2000) compared with Lake Malawi $\delta^{13}C_{alk}$ (open squares) and temperature (gray triangles; Powers et al., 2005) records, and Atlantic meridional sea surface temperature gradient (ΔSST) from the coast of Angola [difference between alkenone-derived SSTs from sediment cores GeoB 6518–1 (05°35.3′S, 11°13.3′E) and GeoB 1023–5 (17°09.5′S, 11°00.5′E); Schefuß et al., 2005]. Note that y axis scales of methane and temperature records are reversed. Vertical dashed line at 11 cal ka indicates transition between in phase and out of phase relationships between the $\delta^{13}C_{alk}$ and CH_4 records. C: Atmospheric carbon dioxide concentrations from TD (Monnin et al., 2001) and January insolation at 10°S (Berger and Loutre, 1991).

[1]GSA Data Repository item 2007200, methods utilized for *n*-alkane $\delta^{13}C$ analysis of core M98-1P, is available online at www.geosociety.org/pubs/ft2007.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

Teeri and Stowe, 1976). Thus, we conclude that vegetation changes in East Africa are mainly driven by changes in aridity, consistent with previous studies of tropical Africa (Schefuß et al., 2003).

We compare the Lake Malawi $\delta^{13}C_{alk}$ record to ice-core methane (CH_4) records from Antarctica and Greenland that mainly reflect inputs from tropical wetlands in the preindustrial period (Brook et al., 2000; Chappellaz et al., 1997). We find that the two data sets closely parallel each other from the LGM until ca. 11 ka (Fig. 2B), the YD being a major feature of both records. At the start of the Holocene, the close correlation between the two records abruptly ends and a more antiphase relationship prevails (Fig. 2B). CH_4 records suggest early Holocene wet conditions, whereas arid conditions were present at Lake Malawi from 11 to 7.7 ka. Variability present in the Lake Malawi $\delta^{13}C_{alk}$ and temperature records (Powers et al., 2005) ca. 8.2 cal ka may be related to Northern Hemisphere cooling at that time (e.g., Thomas et al., 2007), although higher resolution sampling is required to test this idea. CH_4 records indicate drying of the tropics from 7 to 2.5 ka (Chappellaz et al., 1997), but the $\delta^{13}C_{alk}$ record displays the highest percentage of C_3 vegetation at 4.9 ka, signifying wetter conditions in southeast Africa. CH_4 records suggest a return to wetter conditions during the past 2.5 k.y. (anthropogenic methane contributions are also significant during this interval; Chappellaz et al., 1997; Ruddiman and Thomson, 2001), while a shift to increased aridity is observed at Lake Malawi and at other locations in tropical Africa (Gasse, 2000).

The timing of vegetation shifts noted at Lake Malawi generally correlates well with vegetation shifts noted at Lake Rukwa (Vincens et al., 2005) and southern Lake Tanganyika (Vincens, 1991). Ties to conditions in the Southern Hemisphere are also noted, especially during the late Pleistocene, when the Lake Malawi temperature record appears to reflect warming in Antarctica, and possibly the Antarctic Cold Reversal (Powers et al., 2005). Paleoclimate records from South Africa display similarities to the Lake Malawi record and reveal dry conditions during the LGM and early Holocene (Holmgren et al., 2003). Nearby at Lake Masoko, conditions were wet (Fig. 1B) during the LGM and YD (Garcin et al., 2006), when Lake Malawi was arid. Considering the small size of Lake Masoko (area of 0.38 km^2 compared to 22,490 km^2 for Lake Malawi) and its location in the Rungwe volcanic highlands (Fig. 1), it may be more influenced by local orographic effects, whereas Lake Malawi responds more to regional climatic forcing.

Taken together, the $\delta^{13}C_{alk}$ and CH_4 records indicate that arid and wet phases in southeast Africa were in phase with conditions in the global tropics during the late Pleistocene but generally out of phase during the Holocene (Fig. 2B). Ties between Lake Malawi and high-latitude climates have been noted previously and likely result from a combination of changes in global mean temperature and ITCZ variability. The latitudinal position of the ITCZ varies as a result of the interhemispheric temperature contrast, perhaps associated with the bipolar seesaw (Stocker and Johnsen, 2003), with southward displacements occurring during Northern Hemisphere cold periods (Broccoli et al., 2006). Southward ITCZ displacements also may be accompanied by reduced low-latitude convection (Ivanochko et al., 2005). Previous studies of Lake Malawi have provided evidence for southward ITCZ migrations during Northern Hemisphere cold periods, including the YD and Little Ice Age (LIA) (Brown and Johnson, 2005; Filippi and Talbot, 2005; Johnson et al., 2002), and the $\delta^{13}C_{alk}$ record presented here is consistent with these results.

ITCZ migrations have been linked to climate variability in southeast Africa on decadal to millennial time scales and also are thought to occur on longer glacial-interglacial time scales (Broccoli et al., 2006; Ivanochko et al., 2005), but other climate forcings are important and must be considered. Cooler global mean temperatures during the LGM would have led to decreased surface evaporation, resulting in a tendency for increased global aridity, which is noted throughout tropical Africa (Gasse, 2000). Following the LGM, southeast Africa gradually warmed until 13.8 cal ka (Powers et al., 2005), and this temperature increase was accompanied by increased precipitation throughout the African tropics (Gasse, 2000). We suggest that ITCZ variability may have played a role in maintaining the noted in phase relationship between arid and wet conditions in the southeast African tropics with the global tropics during the late Pleistocene. At that time, cool temperatures in the Northern Hemisphere may have caused a southward displacement of the ITCZ (Broccoli et al., 2006), thereby causing the Lake Malawi basin to receive less rainfall, similar to the equatorial and northern tropics. With the collapse of Northern Hemisphere ice sheets, ties between southeast Africa and the northern high latitudes were weakened, perhaps in part due to the ITCZ shifting northward over Africa. Following the early Holocene retreat of Northern Hemisphere ice sheets, the influence of summer insolation on moisture availability in the southern tropics became relatively more important, and antiphased with the northern African tropics. This is apparent from a comparison of austral summer insolation at 10°S (Berger and Loutre, 1991) with the $\delta^{13}C_{alk}$ record (Fig. 2C). The insolation minimum centered at 10 ka corresponds with arid conditions at Lake Malawi and in South Africa (Holmgren et al., 2003), while lakes to the north experienced highstands or overflowing conditions (Gasse, 2000). As insolation increased throughout the Holocene, southeast Africa became wetter. We note arid conditions since 0.5 ka, despite high insolation values. This time period coincides with the LIA, when there is independent evidence for cooler and drier conditions at Lake Malawi, attributed to a southward shift of the ITCZ (Powers, 2005; Brown and Johnson, 2005).

Other forcing mechanisms, such as Atlantic Ocean and Indian Ocean sea surface temperatures (SST), have been linked to rainfall in East Africa (Camberlin et al., 2001; Goddard and Graham, 1999), and such ties are also suggested in the paleorecord. Our $\delta^{13}C_{alk}$ profile tracks the meridional gradient in South Atlantic SSTs off West Africa reasonably well (Fig. 2B), inferring higher rainfall at Lake Malawi when the SST gradient is weak, thereby decreasing southeast trade winds over Africa (Schefuß et al., 2005). This may result in an eastward shift in the north-south–oriented portion of the ITCZ, or IOC, during austral summer, allowing for deeper penetration of Atlantic moisture into East Africa associated with the West African monsoon and more intense rainfall over Lake Malawi. The strength of the southeast trade winds has been linked to conditions in Antarctica, with expansions of sea ice leading to expansions of the Antarctic circumpolar vortex, thereby producing steeper meridional SST gradients and intensifying southeast trade winds (Schefuß et al., 2005; Partridge et al., 2004; Kim et al., 2003). Expansion of the Antarctic circumpolar vortex, associated with cooler and drier conditions, is also an important control on climate in South Africa (Partridge et al., 2004; Holmgren et al., 2003). The links noted between conditions in Antarctica, the Atlantic meridional SST gradient, the strength of the southeast trade winds, and eastward moisture penetration into the African continent likely account for some of the similarities noted in paleoclimate records of South, Central, and East Africa. However, given Lake Malawi's position at the present-day southernmost limit of the ITCZ, the lake is particularly sensitive to shifts in its location.

CONCLUSIONS

This study demonstrates that wet and arid phases in southeast Africa were in phase with conditions in the equatorial and northern tropics during the late Pleistocene (23–11 ka), but out of phase during the Holocene. Arid conditions were present in southeast Africa during the LGM, the YD, in the early Holocene, and during the LIA, whereas peak wet conditions occurred at 13.6 and 4.9 ka. The presence of arid conditions in southeast Africa during the early Holocene is significant, and we note that the frequently used term, African Humid Period, referring to 12–5.5 ka, is inappropriate when considering the climate of a broad expanse of southeast Africa. The late Pleistocene and Holocene climates of southeast Africa were quite variable, both in terms of aridity and temperature. These extreme and abrupt changes in water availability undoubtedly played a significant role in faunal migrations and in the development and collapse of human civilizations.

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REFERENCES CITED

Berger, A., and Loutre, M.F., 1991, Insolation values for the climate of the last 10 million years: Quaternary Science Reviews, v. 10, p. 297–317, doi: 10.1016/0277–3791(91)90033-Q.

Broccoli, A.J., Dahl, K.A., and Stouffer, R.J., 2006, Response of the ITCZ to Northern Hemisphere cooling: Geophysical Research Letters, v. 33, doi: 10.1029/2005GL024546.

Brook, E.J., Harder, S., Severinghouse, S., Steig, E.J., and Sucher, C.M., 2000, On the origin and timing of rapid changes in atmospheric methane during the last glacial period: Global Biogeochemical Cycles, v. 14, p. 559–572, doi: 10.1029/1999GB001182.

Brown, E.T., and Johnson, T.C., 2005, Coherence between tropical East African and South American records of the Little Ice Age: Geochemistry, Geophysics, Geosystems, v. 6, doi: 10.1029/2005GC000959.

Camberlin, P., Janicot, S., and Poccard, I., 2001, Seasonality and atmospheric dynamics of the teleconnection between African rainfall and tropical sea-surface temperature: Atlantic vs. ENSO: International Journal of Climatology, v. 21, p. 973–1005, doi: 10.1002/joc.673.

Chappellaz, J., Blunier, T., Kints, S., Dallenbach, A., Barnola, J.-M., Schwander, J., Rayanud, D., and Stauffer, B., 1997, Changes in the atmospheric CH_4 gradient between Greenland and Antarctica during the Holocene: Journal of Geophysical Research, v. 102, p. 15,987–15,997, doi: 10.1029/97JD01017.

Collister, J.W., Rieley, G., Stern, B., Eglinton, G., and Fry, B., 1994, Compound-specific $\delta^{13}C$ analyses from leaf lipids from differing carbon dioxide metabolisms: Organic Geochemistry, v. 21, p. 619–627, doi: 10.1016/0146–6380(94)90008–6.

Eglinton, G., and Hamilton, R.J., 1967, Leaf epicuticular waxes: Science, v. 156, p. 1322–1335, doi: 10.1126/science.156.3780.1322.

Filippi, M.L., and Talbot, M.R., 2005, Lake Malawi: The paleolimnology of the north basin over the last 25 ky based on the elemental and stable isotopic composition of sedimentary organic matter: Quaternary Science Reviews, v. 24, p. 1303–1328, doi: 10.1016/j.quascirev.2004.10.009.

Garcin, Y., Vincens, A., Williamson, D., Guiot, J., and Buchet, G., 2006, Wet phases in tropical southern Africa during the last glacial period: Geophysical Research Letters, v. 33, doi: 10.1029/2005GL025531.

Gasse, F., 2000, Hydrological changes in the African tropics since the Last Glacial Maximum: Quaternary Science Reviews, v. 19, p. 189–211, doi: 10.1016/S0277–3791(99)00061-X.

Gasse, F., Barker, P., and Johnson, T.C., 2002, A 24,000 yr diatom record from the northern basin of Lake Malawi, *in* Odada, E.O., and Olago, D.O., eds., The East African great lakes: Limnology, palaeolimnology and biodiversity: Netherlands, Kluwer Academic Publishers, p. 393–414.

Goddard, L., and Graham, N.E., 1999, Importance of the Indian Ocean for simulating rainfall anomalies over eastern and southern Africa: Journal of Geophysical Research, v. 104, p. 19,099–19,116, doi: 10.1029/1999JD900326.

Holmgren, K., Lee-Thorp, J.A., Cooper, G.R.J., Lundblad, K., Partridge, T.C., Scott, L., Sithaldeen, R., Talma, A.S., and Tyson, P.D., 2003, Persistent millennial-scale climatic variability over the past 25,000 years in southern Africa: Quaternary Science Reviews, v. 22, p. 2311–2326, doi: 10.1016/S0277–3791(03)00204-X.

Huang, Y., Street-Perrott, F.A., Metcalfe, S.E., Brenner, M., Moreland, M., and Freeman, K.H., 2001, Climate changes as the dominant control on glacial-interglacial variations in C_3 and C_4 plant abundance: Science, v. 293, p. 1647–1651, doi: 10.1126/science.1060143.

Ivanochko, T.S., Ganershram, R.S., Brummer, G.-J.A., Ganssen, H., Jung, S.J.A., Moreton, S.G., and Kroon, D., 2005, Variations in tropical convection as an amplifier of global climate change at the millennial scale: Earth and Planetary Science Letters, v. 235, p. 302–314, doi: 10.1016/j.epsl.2005.04.002.

Johnson, T.C., and Ng'ang'a, P., 1990, Reflections on a rift lake, *in* Katz, B.J., ed., Lacustrine basin exploration: Case studies and modern analogs: American Association of Petroleum Geologists Memoir 50, p. 340.

Johnson, T.C., Barry, S., Chan, Y., and Wilkinson, P., 2001, Decadal record of climate variability spanning the past 700 yr in the southern tropics of East Africa: Geology, v. 29, p. 83–86, doi:10.1130/00917613(2001)029<0083:DROCVS>2.0.CO;2.

Johnson, T.C., Brown, E.T., McManus, J., Barry, S., Barker, P., and Gasse, F., 2002, A high-resolution paleoclimate record spanning the past 25,000 years in southern East Africa: Science, v. 296, p. 113–132, doi: 10.1126/science.1070057.

Kim, J.-H., Schneider, R.R., Mulitza, S., and Muller, P.J., 2003, Reconstruction of SE trade-wind intensity based on sea-surface temperature gradients in the Southeast Atlantic over the last 25 kyr: Geophysical Research Letters, v. 30, doi: 10.1029/2003GL017557.

Leroux, M., 2001, The meteorology and climate of tropical Africa: Chichester, UK, Springer, Praxis Publishing, 548 p.

Livingstone, D.A., and Clayton, W.D., 1980, An altitudinal cline in tropical African grass floras and its paleoecological significance: Quaternary Research, v. 13, p. 392–402, doi: 10.1016/0033–5894(80)90065–4.

Monnin, E., Indermuhle, A., Dallenbach, A., Fluckiger, J., Stauffer, B., Stocker, T.F., Rayaud, D., and Barnola, J.-M., 2001, Atmospheric CO2 concentrations over the Last Glacial Termination: Science, v. 291, p. 112–114, doi: 10.1126/science.291.5501.112.

O'Leary, M.H., 1981, Carbon isotope fractionation in plants: Phytochemistry, v. 20, p. 553–567, doi: 10.1016/0031–9422(81)85134–5.

Partridge, T.C., Scott, L., and Schneider, R.R., 2004, Between Aghulas and Benguela: Response of southern African climates of the late Pleistocene to current fluxes, orbital precession and the extent of the circum-Antarctic vortex, *in* Battarbee, R.W., ed., Past climate variability through Europe and Africa: Dordrecht, Netherlands, Springer, p. 45–68.

Powers, L., 2005, Calibration and application of a new paleotemperature tool in lacustrine systems: TEX_{86} for continental paleoclimate reconstruction [Ph.D. thesis]: Minneapolis, University of Minnesota, 90 p.

Powers, L.A., Johnson, T.C., Werne, J.P., Castañeda, I.S., Hopmans, E.C., Sinninghe Damste, J.S., and Schouten, S., 2005, Large temperature variability in the southern African tropics since the Last Glacial Maximum: Geophysical Research Letters, v. 32, doi: 10.1029/2004GL022014.

Raven, P.H., Event, R.F., and Eichnorn, S.E., 1999, Biology of plants: New York, W.H. Freeman and Company, 875 p.

Ricketts, R.D., and Johnson, T.C., 1996, Early Holocene changes in lake level and productivity in Lake Malawi as interpreted from oxygen and carbon isotopic measurements of authigenic carbonates, *in* Johnson, T.C., and Odada, E.O., eds., The limnology, climatology and paleoclimatology of the east African lakes: Amsterdam, Gordon and Breach, p. 475–493.

Ruddiman, W.F., and Thomson, J.S., 2001, The case for human causes of increased atmospheric CH_4 over the last 5000 years: Quaternary Science Reviews, v. 20, p. 1769–1777, doi: 10.1016/S0277–3791(01)00067–1.

Schefuß, E., Schouten, S., Jansen, J.H.F., and Sinninghe Damsté, J.S., 2003, African vegetation controlled by tropical sea surface temperatures in the mid-Pleistocene period: Nature, v. 422, p. 418–421, doi: 10.1038/nature01500.

Schefuß, E., Schouten, S., and Schneider, R.R., 2005, Climatic controls on central African hydrology during the past 20,000 years: Nature, v. 437, p. 1003–1006, doi: 10.1038/nature03945.

Stocker, T.F., and Johnsen, S.J., 2003, A minimum thermodynamic model for the bipolar seesaw: Paleoceanography, v. 18, doi: 10.1029/2003PA000920.

Teeri, J.A., and Stowe, L.G., 1976, Climatic patterns and the distribution of C_4 grasses in North America: Oecologia, v. 23, p. 1–12.

Thomas, E.R., Wolff, E.W., Mulvaney, R., Steffensen, J.P., Johnsen, S.J., Arrowsmith, C., White, J.W.C., Vaughn, B., and Popp, T., 2007, The 8.2 ka event from Greenland ice cores: Quaternary Science Reviews, v. 26, p. 70–81, doi: 10.1016/j.quascirev.2006.07.017.

Vincens, A., 1991, Late Quaternary vegetation history of the South-Tanganyika Basin. Climatic implications for South Central Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 86, p. 207–226, doi: 10.1016/0031–0182(91)90081–2.

Vincens, A., Buchet, G., Williamson, D., and Taieb, M., 2005, A 23,000 yr pollen record from Lake Rukwa (8°S, SW Tanzania): New data on vegetation dynamics and climate in central East Africa: Review of Palaeobotany and Palynology, v. 137, p. 147–162, doi: 10.1016/j.revpalbo.2005.06.001.

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