Long-term variability and rainfall control of savanna fire regimes in equatorial East Africa

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Abstract

Fires burning the vast grasslands and savannas of Africa significantly influence the global carbon cycle. Projecting the impacts of future climate change on fire-mediated biogeochemical processes in these dry tropical ecosystems requires understanding of how various climate factors influence regional fire regimes. To examine climate–vegetation–fire linkages in dry savanna, we conducted macroscopic and microscopic charcoal analysis on the sediments of the past 25 000 years from Lake Challa, a deep crater lake in equatorial East Africa. The charcoal-inferred shifts in local and regional fire regimes were compared with previously published reconstructions of temperature, rainfall, seasonal drought severity, and vegetation dynamics to evaluate millennial-scale drivers of fire occurrence. Our charcoal data indicate that fire in the dry lowland savanna of southeastern Kenya was not fuel-limited during the Last Glacial Maximum (LGM) and Late Glacial, in contrast to many other regions throughout the world. Fire activity remained high at Lake Challa probably because the relatively high mean-annual temperature (~22 °C) allowed productive C4 grasses with high water-use efficiency to dominate the landscape. From the LGM through the middle Holocene, the relative importance of savanna burning in the region varied primarily in response to changes in rainfall and dry-season length, which were controlled by orbital insolation forcing of tropical monsoon dynamics. The fuel limitation that characterizes the region’s fire regime today appears to have begun around 5000–6000 years ago, when warmer interglacial conditions coincided with prolonged seasonal drought. Thus, insolation-driven variation in the amount and seasonality of rainfall during the past 25 000 years altered the immediate controls on fire occurrence in the grass-dominated savannas of eastern equatorial Africa. These results show that climatic impacts on dry-savanna burning are heterogeneous through time, with important implications for efforts to anticipate future shifts in fire-mediated ecosystem processes.

Keywords: Africa, C4 grasses, charcoal, drought, fire, fuel limitation, grassland, Quaternary, savanna, seasonality

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Introduction

Tropical savanna ecosystems globally cover ~33 million km² (Ramankutty & Foley, 1999) and are highly productive and flammable (Bowman et al., 2009), contributing ~40% of Earth’s annual pyrogenic CO2 emissions (van der Werf et al., 2006; Williams et al., 2007). Most tropical savanna occurs in sub-Saharan Africa, and its emissions alone cause high seasonal and inter-annual variability in global land-atmosphere carbon exchange (Patra et al., 2005; van der Werf et al., 2003; Williams et al., 2007). Vegetation regrowth reduces such short-term variability on decadal timescales (Williams et al., 2007), but during the next century carbon-balance shifts at regional and continental scales may occur depending on how anthropogenic warming influences tropical rainfall regimes, vegetation structure (Hoffmann et al., 2012), and in turn the distribution and frequency of fire in Africa (Williams et al., 2008; Lehsten et al., 2009).

Satellite and long-term field data show that the fires regularly burning the dry, grass-dominated savannas of southern Africa are largely controlled by fuel availability (Lehsten et al., 2009). Wetter conditions typically enhance primary production and accumulation of herbaceous litter, which fuels fires, whereas drier conditions limit primary production and thus fire (Van Wilgen et al., 2004; Archibald et al., 2010b). However, annual rainfall above ~800 mm often impedes fire in African savanna, primarily because the dry season is then not long enough to allow grass fuels to cure and/or for ignition to occur (Krawchuk & Moritz, 2011; Lehmann et al., 2011). Despite the valuable information...
derived from such satellite and field records, our understanding of the climatic drivers of variable fire regimes in African savannas is hampered by the short length of these records (~8 and 20–50 years, respectively), and by the fact that today’s widespread ignition by humans (either deliberate or accidental) weakens the influence of climate variation on fire across major portions of southern and eastern equatorial Africa (Archibald et al., 2010a). In coming decades, this region is expected to experience climate warming, more pronounced rainfall seasonality, and regionally contrasting trends of drying and wetting (Hulme et al., 2001; Tadross et al., 2005; IPCC, 2007). Knowledge of climate–fire linkages is crucial for projecting how these anticipated changes will impact fire-mediated biogeochemical and ecological processes across large portions of tropical Africa.

Paleorecords with linked but independent evidence for shifts in climate, vegetation, and fire enable investigation of the response of fire regimes to a range of climatic changes. For example, paleodata from the grass-dominated ecosystems of the northern Great Plains of North America revealed the predominance of fuel-limited fire regimes during the Holocene (the past 11 700 years); grass production was higher and fires more frequent when conditions were wetter (Nelson et al., 2004; Brown et al., 2005; Grimm et al., 2011). Few paleo-fire records are currently available for evaluating climate–fire linkages in tropical savannas (Power et al., 2008). In Africa, sedimentary charcoal records are often from forested sites at mid-elevations (~2000–3000 m a.s.l) and lack information either on past vegetation change or on rainfall and its seasonality (e.g., Wooler et al., 2003; Finch et al., 2009; Rucina et al., 2009; Tierney et al., 2010). Paleoecological data from tropical South America suggest reduced fire activity in grassland and savanna ecosystems during the LGM and the last glacial–interglacial transition (e.g., Behling et al., 2004, 2005), but these records also lack vegetation-independent paleoclimate data for evaluating the impacts of climate change on fire regimes.

We conducted high-temporal-resolution analysis of macroscopic and microscopic charcoal in the sediments from Lake Challa, a crater lake in equatorial East Africa surrounded by the dry, grass-dominated savanna that is characteristic of the region’s expansive low-elevation plateau areas (Fig. 1a). This lake-sediment record spans the past 25 000 years, a period of major changes in pCO₂, temperature, and moisture balance. Here, we report our charcoal results and compare these results with an exceptionally rich paleoclimate dataset from the same site based on previous geochemical and
geophysical analyses (e.g., Barker et al., 2011; Moernaut et al., 2010, Verschuren et al., 2009). Our objectives are to (1) infer millennial-scale shifts in savanna fire regimes around Lake Challa and within the region, and (2) decipher how these fire-regime shifts are linked to variations in vegetation and climate, especially regional moisture regimes.

Materials and methods

Study site and area

Lake Challa (3.3° S, 37.7° E, 840 m a.s.l.) has a surface area of 4.2 km² and a maximum depth of 94 m. The crater lake fills a steep-sided caldera on the lower southeast slope of Mt. Kilimanjaro. The local climate is tropical semi-arid, with a mean-annual temperature of 25 °C (monthly means ranging 23–27 °C), mean maximum daytime temperature of 30.5 °C (monthly means ranging 28–33 °C), and mean-annual precipitation of 580 mm/yr (Fig. 1b). The interannual variability in rainfall is pronounced, with a range of 330–1050 mm over the period 1978–2005. The evaporation rate of lake-surface water (1700 mm/yr; Payne, 1970) exceeds mean-annual precipitation threefold, underscoring the strongly negative balance of effective moisture in the Lake Challa area. The water level of Lake Challa is stabilized by subsurface inflow derived from rain percolating through forest soils on the higher slopes of Mt. Kilimanjaro (Fig. 1c and d); these inflows account for ~80% of the total annual water input to the lake (Payne, 1970; Verschuren et al., 2009).

The equatorial region of Lake Challa experiences twice-yearly passage of the intertropical convergence zone (ITCZ), creating a strongly bimodal pattern of seasonal rainfall. South-easterly monsoon winds bring ‘long’ rains from March to May (MAM), whereas northeasterly monsoon winds bring ‘short’ rains from October to December (OND). MAM and OND rainfall, on average, account for 48 and 31% of the annual total (Fig. 1b), but with substantial interannual variability in their respective contributions, and occasional ‘failure’ of one or the other rain season. Located east of the Congo Air Boundary year-round, the Lake Challa region is isolated from Atlantic Ocean influence, and the Indian Ocean is its sole source of moisture. This results in an extended main dry season from June through mid-October, which is also the dominant fire season today throughout southern Africa (Archibald et al., 2010b). With >70% of annual rainfall concentrated in the 5 months of March–May and November–December, the total local dry-season length is about 7 months (Archibald et al., 2010b).

Natural vegetation in the wider landscape around Lake Challa is dominated by open bush and grass savanna, with scattered woodland trees and shrubs amounting to 5–10% tree cover (Di Gregorio, 2002). The northern and western outer slopes of the caldera support a small dry-savanna woodland (15–40% tree cover) dominated by Acalypha and Acacia species (Hemp, 2006). Within the steep-sided crater catchment, which encompasses only 1.4 km² excluding the lake, soils are typically thin and rocky. A fringe of evergreen forest occurs along the lakeshore, a dry ‘succulent’ forest with Commiphora baluensis, Haplocoelum foliosum, and Euphorbia bussei occupies the steep middle slopes, and grassland with scattered shrubs occurs immediately below the crater rim. Grasses using C₄ photosynthesis dominate at lower elevations in the region and give way to C₃ grasses above ~2000 m (Tieszen et al., 1979).

Fire in today’s regional landscape is generally fuel-limited, as expected when annual rainfall is well below ~800 mm (Lehmann et al., 2011). Observations based on Moderate Resolution Imaging Spectroradiometer (MODIS) data suggest an average fire-return interval on the order of 5–10 years (Archibald et al., 2009; Lehmann et al., 2011). Rapidly intensifying human activity throughout East Africa in recent decades has led to more frequent and smaller fires than would naturally occur (Archibald et al., 2010b).

Although hominins have inhabited East Africa for millions of years (White et al., 2009) and are thought to have affected its fire regimes for thousands of years at least (Archibald et al., 2012), human impacts on the landscape surrounding Lake Challa have been limited to the last few centuries. These impacts began when permanent settlements developed along the slave and trade routes starting inland from Mombasa on the Indian Ocean coast (Håkansson, 1995; Spear, 1997, Stump & Tagseth, 2009). Pastoralist Maasai, thought to have inhabited the general area for up to ~1800 years (Marshall, 2000), have been very few in number for most of this period (Lane, in press), whereas early agriculturalist settlements in the eastern Mt. Kilimanjaro region starting ~1000 years ago (e.g., Nurse, 1979; Håkansson, 2007) were confined to the mountain’s mid-elevation slopes.

Sediment cores and chronology

Overlapping and cross-correlated piston cores taken from Lake Challa in 2003 and 2005 together form a composite sediment sequence of ~20.8 m (Verschuren et al., 2009). Its chronology is tightly constrained by a high-resolution sequence of accelerator mass spectrometry (AMS) ¹⁴C dates on bulk organic matter, anchored by ²¹⁰Pb dating of recent sediments and corrected for an evolving old-carbon age offset (Verschuren et al., 2009; Blaauw et al., 2011). For the age-depth model used in the present study (named “Challa-chron-2010”), ¹⁴C dates were calibrated using IntCal09 (Reimer et al., 2009) and the spline-smoothing parameter (Blaauw et al., 2011) was set to 0.7. This value yields approximately twofold variation in sedimentation rate throughout the past 25 000 years, which is realistic given the relatively uniform sediment composition and mean thicknesses of varves throughout the sequence (Wolli et al., 2011). We confirmed that within the range of 0.4–0.9, the exact value of the smoothing parameter has no effect on the broad trends in charcoal accumulation rates (CHAR) through time.

Charcoal analysis

Sediment subsamples for macroscopic (>180 µm) and microscopic (<212 µm) charcoal analysis were prepared from known volumes of sediment, as previously described (i.e.,
Tinner & Hu, 2003; Nelson et al., 2006). Macroscopic charcoal particles were counted at 20X magnification using a dissecting microscope. Microscopic charcoal particles were counted on pollen slides under 400X magnification using a Nikon E400 microscope. The mean temporal resolutions of our macro- and micro-charcoal records were 12 and 163 years, respectively. Charcoal concentrations were multiplied by sediment accumulation rates for conversion into CHAR. Macroscopic particles from relatively small basins such as Lake Challa typically derive primarily from fires within ca. 0–5 km of the lakeshore (Peters & Higuera, 2007; Duffin et al., 2008), whereas microscopic charcoal particles can derive from fires up to 20–100 km away (Clark, 1988; Tinner et al., 1999). The majority of the catchment is within <300 m of the lakeshore, which means that macroscopic charcoal at Lake Challa likely derives from fires occurring both within, and immediately outside of, the crater. As volcanic soils in this area are thin and rocky with poor water-holding capacity, the landscape within the source area of macroscopic charcoal is (and probably has always been) somewhat drier than the wider lowland region surrounding the crater, from which the microscopic charcoal is derived.

The fire-return interval for grassland and savanna ecosystems in equatorial Africa ranges between about 5 and 10 years (Archibald et al., 2010b). Given that the contiguous 1 cm sampling interval for our macroscopic charcoal analysis integrates 8–18 years of accumulation (Blauwe et al., 2011), we cannot distinguish individual fire events from background charcoal accumulation in the sediments. This situation is similar to that in fire records from lake archives in the grass-dominated ecosystems of North America (Brown et al., 2005; Nelson et al., 2006). In these circumstances, CHAR reflects changes in the prevalence of fire at longer time scales, which is controlled by factors such as fuel availability, fuel moisture, vegetation type, and/or ignition frequency. In the Lake Challa record, stratigraphic patterns in CHAR are similar to those of the absolute charcoal concentrations (Fig. S1), indicating that temporal trends in CHAR are not simply driven by variation in sediment accumulation rate through time.

Statistical analyses

We used detrended correspondence analysis (DCA) to summarize the main stratigraphic trends observed in the pollen data from Lake Challa (van Geel et al., 2011), including only taxa with >2% abundance in at least one sample. Cyperaceae was excluded from the pollen sum because in East Africa its pollen is thought to be primarily of aquatic origin (e.g., Vincens et al., 2005), and Euphorbia was excluded from the ‘Woodland’ subtaxon pollen sum because it must be derived from the highly local Euphorbia bussei forest occupying steep cliffs inside the crater. Percent abundances of the remaining taxa were recalculated prior to performing DCA in PAST (version 2.0.4, Hammer et al., 2001).

To assess the effects of climatic and vegetational changes on fire regimes, we performed correlation analysis of CHAR with various geochemical and pollen records (described below). For example, a significant positive correlation between moisture availability and the rate of charcoal accumulation may suggest that fuel availability limits burning, whereas the opposite may suggest that wet conditions directly limit fire activity. For the correlation analysis, all time series were resampled to the temporal resolution of the indicator with lowest time resolution (micro-CHAR). The significance of these correlations was evaluated with a block bootstrap to account for temporal autocorrelation (Gavin et al., 2011), using the R software package (R Core Development Team 2011).

Paleoclimate context

Previous geophysical and geochemical analyses of the Lake Challa sediment record have yielded a wealth of paleoclimate information (e.g., Barker et al., 2011; Moernaut et al., 2010, Tierney et al., 2011, Verschuren et al., 2009; Wolff et al., 2011). These data are key to evaluating the climatic controls of fire-regime shifts inferred from our charcoal data. The primary records of hydroclimatic variation at Lake Challa are the BIT (Branched and Isoprenoid Tetraether) index and the δ18O of diatom frustules (δ18O_diatom, Fig. 2). BIT values are a positive function of the amount of annual rainfall (Verschuren et al., 2009); δ18O_diatom is negatively related to annual moisture balance (precipitation minus evaporation), with a strong imprint of the length and severity of the main dry season (Barker et al., 2011).

Variations in BIT and δ18O_diatom at Lake Challa indicate that marked and partly decoupled variation in the amount and seasonality of rainfall occurred in equatorial East Africa during the past 25,000 years. These variations were primarily driven by tropical monsoon dynamics associated with precessional (∼21 000-year-period) changes in low-latitude insolation (Verschuren et al., 2009). The overall trends in δ18O_diatom track those of BIT, except during the two periods (∼25.0–20.5 and 5.0–0.0 kyr bp) when the orbital configuration and thus annual distribution of insolation weakened the southeastern monsoon (Fig. 2). A weakened monsoon reduced the amount of rainfall during the long rain season, thereby enhancing the intensity of evaporation and/or length of the main dry season (Barker et al., 2011).

Before ∼20.5 kyr bp, BIT values were relatively high (0.66, on average) but variable, suggesting wet conditions caused by an enhanced northeasterly monsoon in response to a large summer/winter interhemispheric insolation gradient (Verschuren et al., 2009). Simultaneously, δ18O_diatom values were relatively high (39.5% on average), because of an especially long main dry season (Barker et al., 2011). From 20.5 to 15.0 kyr bp BIT was low (0.37, on average), whereas δ18O_diatom values display little change compared with the period 25–20.5 kyr bp. This indicates low total annual rainfall, as neither monsoon was enhanced and minimum equatorial insolation in September further reduced OND rains (Fig. 2).

From 15 kyr bp, increasing BIT and decreasing δ18O_diatom indicate a trend toward less severe seasonal aridity. Excluding the arid Younger Dryas period (YD, ∼13.3–11.7 kyr bp in equatorial East Africa; Verschuren et al., 2009), BIT values were high (0.73, on average) throughout the period 15.0–9.0 kyr bp, while δ18O_diatom values were low (38.2% on average). These data indicate high annual rainfall and reduced seasonal aridity resulting from an enhanced southeastern
monsoon. Both BIT and δ18O_diatom reached peak values in the period ~11.5–9.0 kyr bp. The shifts to lower BIT values and higher δ18O_diatom values ~9.0 kyr bp signify a reduction in annual moisture, probably because a weakening southeastern monsoon and minimum in March insolation reduced MAM rainfall (Verschuren et al., 2009; Barker et al., 2011).

From ~5.0 kyr bp to the present, generally high BIT values (0.69, on average) indicate higher annual rainfall, whereas the highest δ18O_diatom values (40.3‰, on average) of the entire record suggest pronounced seasonal aridity. Rainfall increased mostly during OND as a result of an intensifying northeastern monsoon, but the length and/or severity of the dry season also increased because a weak southeastern monsoon shortened the MAM rainy season (Barker et al., 2011). Other hydroclimatic records from East Africa mostly suggest that aridity increased during the late Holocene (e.g., Russell & Johnson, 2005; Garcin et al., 2012). Despite similar seasonal patterns of rainfall and drought in the periods 25–20.5 and 5.0–0.0 kyr bp, the absolute BIT and δ18O_diatom values suggest that the latter period was drier than the former. Barker et al. (2011) propose that ~2–3 °C higher annual temperatures during the late Holocene relative to full glacial time (Fig. 2, Tierney et al., 2008) must have increased evaporation and thus decreased overall moisture availability during the late Holocene.

**Paleovegetation context**

To infer the effects of vegetation changes on fire regimes, we summarize here paleovegetation data from Lake Challa, including pollen assemblages indicative of the regional vegetation (van Geel et al., 2011) and δ13C of terrestrial plant leaf-waxes indicative of the relative abundance of C3 and C4 plant biomass within the crater (Sinninghe Damsté et al., 2011). Grass pollen consistently exceeded 60%, and often 70%, throughout the past 25 000 years, suggesting that grasses have always dominated the regional landscape. Although before ~15.0 kyr bp the pollen abundance of Afrotomante trees was relatively high their contribution to the total pollen sum was mostly ~25% (Fig. 3). Today Afrotomante taxa mostly occur in wet habitats above 2000 m a.s.l. on Mt. Kilimanjaro (>20 km from Lake Challa), and they consistently represent >40% of the surface-sediment pollen assemblages from within the montane forest (e.g., Rucina et al., 2009). Thus, the Afrotomante Belt was likely farther down slope of its current location on Mt. Kilimanjaro prior to ~15.0 kyr bp, but trees and shrubs remained scarce in the immediate vicinity of Lake Challa. Woody plants were rare both locally and regionally before ~15.0 kyr bp. This probably resulted from the low pCO2 during glacial time (Fig. 3), which has been suggested to cause carbon starvation (Ward et al., 2005; Gerhart et al., 2012) and slow regrowth following fire (Bond et al., 2003; Beerling & Osborne, 2006).

Pollen from Afrotomante taxa decreased to 10–15% by the early Holocene and further to ~5% in the late Holocene, presumably reflecting gradual upward retreat of Mt. Kilimanjaro’s montane forest zone. The woodland pollen sum, which includes trees such as Ficus and Lannea commonly found in today’s riparian forest fringe surrounding Lake Challa, reached peak values of only 15% during the Holocene. Therefore, woody taxa remained generally rare in the wider grass-dominated landscape around Lake Challa during the Holocene, and it is unlikely that the region ever transitioned to a mesic savanna where fire or other disturbances are required to prevent canopy closure (Sankaran et al., 2005; Archibald et al., 2009).

Consistent with the pollen record, high leaf-wax δ13C values (~23 to −24‰) suggest that trees and shrubs were largely absent inside the crater prior to ~15.0 kyr bp (Sinninghe et al., 2011; van Geel et al., 2011). Leaf-wax δ13C data reveal a transition to mixed C3/C4 vegetation within and around the crater between ~15 and 11 kyr bp, since at that time C4 plants declined from a ~85 to ~50% contribution to leaf waxes (Fig. 3). This transition was interrupted by the YD when C4 plants, presumably mostly C4 grasses as suggested by the high
tion rate data and atmospheric along with the microscopic and macroscopic charcoal accumula-
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executed in preparation of detailed morphological screening of charcoal particles neither our own qualitative observations or the more Lake Challa during the past 25,000 years. However, Major fluctuations in macro- and micro-CHAR occur at values of grass pollen, temporarily returned to abundances close to those of the glacial period.

Results

Major fluctuations in macro- and micro-CHAR occur at Lake Challa during the past 25,000 years. However, neither our own qualitative observations or the more detailed morphological screening of charcoal particles executed in preparation of \(^{14}\)C dating (Blaauw et al., 2011) suggest that plants other than grasses ever contributed significantly to the macroscopic charcoal recovered from the Lake Challa sediment record. Furthermore, the \(^{13}\)C values of 22 samples of \(^{14}\)C-dated charcoal particles from throughout the Lake Challa sequence show that all except one ambiguous sample are derived predominantly from C\(_4\) grasses (Blaauw et al., 2011). Prior to ~15.0 kyr bp, the values of both macro- and micro-CHAR vary greatly but are relatively high (Fig. 2). Macro- and micro-CHAR are generally lower from 25 to 20.5 kyr bp (on average 4.2 and 1.8 \(\times\) 10\(^4\) particles cm\(^{-2}\) yr\(^{-1}\)), respectively) than from 20.5 to 15.0 kyr bp (on average 4.9 and 3.0 \(\times\) 10\(^4\) particles cm\(^{-2}\) yr\(^{-1}\), respectively). Compared to the nearly twofold average increase in micro-CHAR from 25–20.5 to 20.5–15.0 kyr bp, the increase in macro-CHAR is more modest. Macro-CHAR is not significantly correlated with either BIT or \(^{18}\)O\(_{\text{diatom}}\) between 25 and 15 kyr bp (Fig. 4). In contrast, micro-CHAR is correlated negatively with BIT (\(r = -0.62, P < 0.001, n = 42;\) Fig. 4) and positively with \(^{18}\)O\(_{\text{diatom}}\) (\(r = 0.36, P < 0.05, n = 42;\) Fig. 4).

Between 15.0 and 9.0 kyr bp, macro-CHAR is variable but generally high (5.0 particles cm\(^{-2}\) yr\(^{-1}\)), on average) while micro-CHAR exhibits large fluctuations with minimum values (1.8 \(\times\) 10\(^4\) particles cm\(^{-2}\) yr\(^{-1}\), on average) similar to those of 25–20.5 kyr bp. Values of macro- and micro-CHAR are generally low during the YD (Fig. 2). From 15 to 9 kyr bp, excluding the YD, macro-CHAR displays a strong positive correlation with BIT (\(r = 0.65, P < 0.002, n = 20;\) Fig. 4) and a negative, weaker correlation with \(^{18}\)O\(_{\text{diatom}}\) (\(r = -0.42, P = 0.06, n = 20;\) Fig. 4). During this time, micro-CHAR is correlated negatively with BIT (\(r = -0.73, P < 0.001, n = 20;\) Fig. 4) and positively with \(^{18}\)O\(_{\text{diatom}}\) are (\(r = 0.81, P < 0.001, n = 20;\) Fig. 4).

Between 9.0 and 6.0 kyr bp, the macro-CHAR values are moderate (3.4 particles cm\(^{-2}\) yr\(^{-1}\), on average) whereas micro-CHAR displays a broad peak (2.2 \(\times\) 10\(^4\) particles cm\(^{-2}\) yr\(^{-1}\), on average). After ~6.0 kyr bp, micro-CHAR and macro-CHAR decline to their lowest levels of the past 25,000 years (Fig. 2), and remain relatively low but variable until the present (on average 0.7 \(\times\) 10\(^3\) and 2.0 particles cm\(^{-2}\) yr\(^{-1}\), respectively). For the period 9.0–0 kyr bp, micro-CHAR is negatively correlated with BIT (\(r = -0.53, P < 0.005, n = 42;\) Fig. 4) and \(^{18}\)O\(_{\text{diatom}}\) (\(r = -0.55, P < 0.001, n = 40;\) Fig. 4). Likewise, macro-CHAR is negatively correlated with BIT (\(r = -0.32, P < 0.05, n = 41;\) Fig. 4) and \(^{18}\)O\(_{\text{diatom}}\) (\(r = -0.42, P < 0.05, n = 40;\) Fig. 4).

Discussion

The linked and chronologically secure reconstructions of fire, climate, and vegetation from Lake Challa over
the past 25,000 years allow us to infer patterns and controls of long-term fire-regime dynamics in the dry grass-dominated savanna of equatorial East Africa. These data suggest that fire-regime shifts in this region were primarily driven by variation in both the total amount and seasonality of annual rainfall. This moisture-regime variation was in turn driven by changes in insolation forcing, but modified by glacial-to-interglacial temperature shifts.

Values of micro-CHAR and macro-CHAR were overall high prior to ~15 kyr bp at Lake Challa, indicating high fire activity in the region. This finding is striking, because worldwide most charcoal records extending to the last-glacial period display low fire activity compared to the Holocene (Behling et al., 2005; Power et al., 2008; Daniau et al., 2010; Mooney et al., 2011), presumably because low pCO$_2$ and colder, drier conditions tended to reduce fuel production (Daniau et al., 2010).

At Lake Challa, micro-CHAR is correlated negatively with BIT and positively with $\delta^{18}$O$_{diatom}$ from 25.0 to 15.0 kyr bp, suggesting greater fire activity when rainfall was low and moisture deficits high during the main dry season, opposite the expectation for fuel-limited conditions. Thus, glacial-era fuel limitation did not

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Fig. 4 Correlations of micro-CHARs and macro-CHARs at Lake Challa with BIT and $\delta^{18}$O$_{diatom}$ during the indicated time periods. Data from the Younger Dryas period (13.3–11.7 kyr bp at Lake Challa) are excluded from the 15–9 kyr bp regressions. The gray and dashed lines are the 95% confidence and prediction intervals, respectively.

extend to the region around Lake Challa, where climate and vegetation appear to have sustained frequent savanna burning. The mean-annual temperature of ~22°C experienced by the lowlands of equatorial Africa during glacial time (Tierney et al., 2008) corresponds to today’s mean-annual temperature at ~10° North or South latitude, which in Africa is still well within the tropical savanna biome. Therefore, vegetation and fuel production were likely not temperature-limited during the glacial period. Furthermore, C₄ grasses use water efficiently (e.g., Taylor et al., 2010) and are not limited by low pCO₂ (Kgope et al., 2010), consequently their dominance during the glacial period at Lake Challa (Fig. 3) may have prevented fuel limitation. Unlike micro-CHAR, macro-CHAR is not correlated with BIT or δ¹⁸O_diatom between 25.0 and 15.0 kyr bp (Fig. 4), suggesting that fuel limitation may have occurred in the local area possibly because the thin rocky soils within the Lake Challa watershed resulted in low grass biomass production.

Prior to ~15.0 kyr bp, millennial-scale fluctuations in regional fire activity may be related to shifts in the amount and seasonal distribution of annual rainfall. For example, micro-CHAR was relatively low and BIT relatively high between 25.0 and 20.5 kyr bp (Fig. 2), which suggests that moist conditions limited fire occurrence. In this semi-arid region where only a few weeks of dry weather are required to produce highly flammable fuels (Stott, 2000), it is unlikely that dry-season aridity was reduced to the extent that grass fuels lacked sufficient drying time. Instead, wet conditions probably effectively shortened the fire season and reduced the probability of ignitions before 20.5 kyr bp. Conversely, drier conditions associated with reduced rainfall from 20.5 to 15.0 kyr bp (Verschuren et al., 2009; Barker et al., 2011) probably lengthened the fire season and led to more burning in the region, as indicated by elevated micro-CHAR values.

Effective moisture continued to exert primary control over millennial-scale variations in fire activity during the last glacial-interglacial transition (15.0–9.0 kyr bp). For example, micro-CHAR was correlated negatively with BIT and positively with δ¹⁸O_diatom from 15.0 to 9.0 kyr bp (excluding the YD), suggesting more regional burning during periods of reduced rainfall and greater moisture deficits. In contrast to micro-CHAR, macro-CHAR is correlated positively with BIT and negatively with δ¹⁸O_diatom. This pattern suggests that increased rainfall during 15.0–9.0 kyr bp led to more local burning, implying fuel limitation of fire activity at local scales. The expansion of woody biomass around Lake Challa between 15.0 and 9.0 kyr bp (Fig. 3), which probably occurred as the result of increased pCO₂, could also have favored local fire activity. However, that these woody plants would have contributed significantly to charcoal abundance is inconsistent with morphological charcoal characterization, charcoal δ¹³C data, and pollen assemblages, which all suggest a largely grass-fueled fire regime throughout the past 25 kyr.

During the YD, annual rainfall declined, seasonal aridity increased, and vegetation composition immediately around Lake Challa reverted to a glacial-like state (Fig. 2 and Fig. 3, Sinninghe et al., 2011; Verschuren et al., 2009). The low values in our macro-CHAR record (Fig. 3) may indicate an exacerbation of ongoing local fuel limitation. However, low fire activity across the region as inferred from micro-CHAR (Fig. 3) cannot be easily attributed to fuel limitation, which did not occur during the LGM and the late-glacial period when climate and vegetation conditions were similar to those of the YD. An alternative explanation is that failure of the African monsoon during the cool and dry YD (Garcín et al., 2007; Talbot et al., 2007) decreased atmospheric convection, which could have reduced lightning strikes and fire ignitions.

The fuel-limited state that characterizes today’s fire regimes of the dry, grass-dominated savannas in East Africa appears to have begun around 5000–6000 years ago. The mean micro- and macro-CHAR values of the past six millennia were the lowest of the past 25 000 years, and coincided with severe dry-season aridity during most of this period (Fig. 2, Barker et al., 2011). Negative correlations of micro- and macro-CHAR with δ¹⁸O_diatom between 9.0 and 0 kyr bp also suggest reduced fire activity being related to increased seasonal aridity (Fig. 4), supporting our inference of reduced fire activity being related to increased seasonal aridity (Fig. 4), supporting our inference of fuel limitation after ~6.0 kyr bp. However, decreased burning ~6.0 kyr bp inferred from micro- and macro-CHAR also coincides with a BIT-inferred shift to slightly higher annual rainfall (Figs 2 and 4), which seems to argue against late-Holocene fuel limitation. We suggest that although intensified ‘short’ rains caused relatively high total annual rainfall at that time (Fig. 2; Barker et al., 2011; Verschuren et al., 2009), enhanced dry-season evaporation created a severe moisture deficit that reduced grass biomass production and facilitated the onset of a fuel-limited fire regime. Other paleoclimate records from the lowlands of East Africa also indicate severe late-Holocene aridity. For example, Lake Turkana in northwestern Kenya declined by ~50 m around 5.3 kyr bp and remained generally low during the late Holocene (Garcín et al., 2012).

The region’s savanna became fuel-limited during the late Holocene but not during the period 25–20.5 kyr bp despite similar seasonal patterns of insolation (Fig. 2). This contrast implies that higher temperatures during
the late Holocene accentuated the severity of prolonged seasonal drought (Barker et al., 2011). Therefore, the fuel-limited nature of fire in many modern-day lowland African savannas (Lehsten et al., 2009; Archibald et al., 2010a; Krawchuk & Moritz, in press) is caused partially by hot tropical lowland conditions, instead of solely by low rainfall or prolonged seasonal drought. These results, combined with evidence for human impacts in the immediate region around Lake Challa being limited to the last few centuries (Hákansson, 2007; Stump & Tagseth, 2009; Lane, in press), may also indicate that late-Holocene fuel limitation of fire began thousands of years before humans became established in the area.

The fuel-limited conditions during the late Holocene inferred from our Lake Challa data did not extend throughout the tropics. For example, in South America forest expanded after ~5 kyr bp throughout grassland and savanna ecosystems probably in response to an increasingly wet climate (Silva et al., 2008, 2011; Silva & Anand, 2011), leading to reduced activity of natural fires (Behling et al., 2004). Evidence from Lake Rutundu on Mt. Kenya indicates that even within East Africa the fire regime at high-mountain elevations was limited by poor vegetation flammability in response to the expansion of woody plants into alpine grasslands after ~5 kyr bp (Wooller et al., 2003; Street-Perrott et al., 2008). Together these data suggest that the direct influence of distinct hydroclimatic factors on fire regimes is most apparent when changes in vegetation composition are not dramatic, such as in lowland savanna surrounding Lake Challa.

The temporal variation in climate controls on fire which we documented in this study is consistent with the observation that present-day spatial variations in the fire regime, woody cover, and primary production of African savannas are mainly related to the amount and seasonal concentration of rainfall (Bucini & Hanan, 2007; Williams et al., 2008; Ciais et al., 2009; Good & Caylor, 2011; Lehmann et al., 2011). Our results from Lake Challa reveal that, under similar conditions of insolation-driven monsoon dynamics, the relatively modest glacial-to-interglacial temperature increase (~3 °C) led to reduced fuel production in African lowland savanna and grassland. Climate models suggest that both mean-annual temperature and precipitation will increase throughout East Africa in the coming century (IPCC, 2007). Additional warming would further promote fuel limitation of fire, at least when local human interference in ignition frequency is limited (Archibald et al., 2010a). This fuel limitation may be overturned if projected increases in precipitation (IPCC, 2007) effectively increase moisture availability for plant growth. Such uncertainty combined with the spatially variable influence of rainfall and seasonality on fire, make projecting how future climatic changes may influence the fire regime of African savannas an ongoing challenge.

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References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Microscopic and macroscopic charcoal concentration and influx data from Lake Challa (5-sample moving averages).

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