Effect of aridity and rainfall seasonality on vegetation in the southern tropics of East Africa during the Pleistocene/Holocene transition

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ABSTRACT

Fossil pollen analyses from northern Lake Malawi, southeast Africa, provide a high-resolution record of vegetation change during the Pleistocene/Holocene transition (~18–9 ka). Recent studies of local vegetation from lowland sites have reported contrasting rainfall signals during the Younger Dryas (YD). The Lake Malawi record tracks regional vegetation changes and allows comparison with other African records identifying vegetation opening and local forest maintenance during the YD. Our record shows a gradual decline of afrotropical vegetation at 18 ka. Around 14.5 ka, tropical seasonal forest and Zambezian miombo woodland became established. At ~13 ka, drier, more open formations gradually became prevalent. Although tropical seasonal forest taxa were still present in the watershed during the YD, this drought-intolerant forest type was likely restricted to areas of favorable edaphic conditions along permanent waterways. The establishment of drought-tolerant vegetation followed the reinforcement of southeasterly tradewinds resulting in a more pronounced dry winter season after ~11.8 ka. The onset of the driest, most open vegetation type coincided with a lake low stand at the beginning of the Holocene. This study demonstrates the importance of global climate forcing and local geomorphological conditions in controlling vegetation distribution.

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Introduction

The African Tropics, which today play a major role in the global hydrological cycle, have undergone tremendous changes over the last 20,000 yr (Gasse, 2000). As the distribution of tropical African vegetation is largely constrained by regional hydrology, past climate changes are often associated with reorganizations of biome distribution (Gajewski et al., 2002; Gasse et al., 2008). However, vegetation response to climate change is poorly understood. Southeast African vegetation is particularly sensitive to changes in precipitation and rainfall seasonality (Hély et al., 2006) resulting from complex interactions between the African Monsoon, Intertropical Convergence Zone (ITCZ), and Congo Air Boundary (CAB; Figure 1; Leroux, 2001). Changes in regional vegetation recorded in high-resolution lake sediment cores can serve as a useful tool for deciphering long-term as well as abrupt seasonal changes in these important circulation patterns.

Although paleoclimate and vegetation records in tropical Africa during the last glacial termination are in close agreement until ~13 ka, changes during the Younger Dryas (YD) interval are unclear and vary regionally (Gasse et al., 2008). In much of North Africa, an abrupt return of aridity is observed resulting from a southward ITCZ displacement, and vegetation cover was greatly reduced (Hooghmiestra, 1988; Zhao et al., 2000). In contrast, rainforests remained significant until the early Holocene in coastal southwestern Africa (Dupont and Behling, 2006).

Multi-proxy analysis of sediments covering the YD chronozone (13–11.8 ka) from Lake Malawi (9°14′S, 3°41′E) have suggested a return to drier, cooler conditions and intense northeasterly (NE) tradewinds (Filippi and Talbot, 2005; Powers et al., 2005; Barker et al., 2007; Brown et al., 2007; Castañeda et al., 2007; Woltering et al., 2011). Although this points to climatic conditions in southeast Africa similar to those farther north, the vegetation record of the YD in southeast Africa is not as straightforward. Recent studies from Lake Masoko (9°20′S; 840 m asl; Figure 1), a small maar lake within the Lake Malawi watershed located less than 100 km from the northern lakeshore, document an expansion of tropical seasonal forest during the YD corresponding with a shortened dry season (Garcin et al., 2006, 2007; Vincens et al., 2007a).

Because of the small size (<1 km²) and morphometry of Lake Masoko, it is difficult to differentiate local (<1 km²) signals from regional (>1 km²) signals in the pollen record. In order to understand the local increase in drought-intolerant forest given regionally drier conditions, comparison with a regional vegetation record is essential. However, until now Lake Masoko has provided the only continuous high-resolution record of vegetation capable of capturing abrupt events in southeast Africa during this climatic transition.
Lake Malawi drill core MAL05-2A sediments provide a continuous, high-resolution record of changing vegetation in a large watershed (65,000 km²) from 18 to 9 ka, which make this record conducive for capturing both rapid and gradual environmental changes at a regional scale (Brown et al., 2007). Lake Malawi is located at the modern southern extent of the ITCZ, rendering it climatically sensitive to shifts in atmospheric circulation observed by previous studies of the Lake Malawi Scientific Drilling Project (Figure 1; Brown et al., 2007; Cohen et al., 2007; Scholz et al., 2007; Scholz et al., 2010).

Here pollen analyses are presented from the north basin of Lake Malawi in order to better understand the relationship between regional vegetation shifts and abrupt climatic events. The situation of Lake Masoko within the greater Malawi watershed and its proximity (~100 km) to the Malawi lakeshore ensures that both lakes are influenced by similar regional climatic conditions (Figure 1). In particular, the ongoing debate (Brown et al., 2007; 2008; Garcin et al., 2008) about the effect of the YD on hydrology and vegetation distribution in southeast Africa can be resolved by the comparison of our record with the signal observed at Lake Masoko.

Modern setting and implications for palynology

Lake Malawi is the southernmost lake in the East African Rift Valley and lies in a series of half-grabens. It is permanently stratified, with anoxic conditions below 250 m, and is drained by the Shire River to the south (Eccles, 1974). The watershed rises steeply from the lake (478 m asl) and is immediately bordered by mountains to the north and west with elevations of 3000 m in the Rungwe Highlands and Nyika Plateau (Malawi Government, 1983).

The distribution of most vegetation in tropical Africa is controlled by rainfall and rainfall seasonality, although temperature is also a constraint in high altitudes (Polhill, 1966; White, 1983; Hély et al., 2006). Within the Lake Malawi watershed, mean annual precipitation (MAP) ranges from 800 mm/yr in the lowlands to 2400 mm/yr on the slopes of Rungwe Highlands (Debusk, 1994). High rainfall in the highlands feeds rivers that are an important source of pollen to the northern basin. A single rainy season occurs November–April when prevailing surface winds are northeasterly (NE), marking the passage of the ITCZ (Figure 1). May–October is the dry season, dominated by strong southeasterly (SE) tradewinds (Malawi Government, 1983).

Lowland vegetation surrounding Lake Malawi (<1500 m asl) is comprised of both wetter and drier Zambezian woodlands, growing in areas with more or less than 1000 mm/yr, respectively (Figure 1; White, 1983). These low diversity woodlands include mainly deciduous species of Uapaca, Brachystegia, Isoberlinia, Julbernardia, and Combretaceae, all of which tolerate a long dry season (>6 months). Drier locations display more open canopies and higher proportion of grasses and Combretaceae. Flooded grasslands with Cyperaceae and Typha are present at the lakeshore and along the Songwe River. Closed canopy, drought-intolerant tropical seasonal forests with trees like Myrica, Macaranga, Ulmaceae, and Moraceae, and shade-loving herbs (Urticaceae) are not widespread but occur in the low to mid-altitudes, in areas with moister edaphic conditions and poor drainage such as along streams (Polhill, 1966). Many species of fern are also common along rivers and streams. Above 1500 m, afromontane grasslands in areas north of the lake are interrupted by discontinuous patches of afromontane forests, whose composition varies with rainfall. Olea capensis is typical of moister forest assemblages (1500–2000 mm/yr; 0–3 dry months) from 1500 to 2500 m, whereas

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Podocarpus, Juniperus, Ericaceae and Olea africana are common above 2000 m in drier sites (800–1700 mm/yr; ~4 dry months; White, 1983). Grasslands are widespread at all elevations, but are concentrated at the southern end of the lake where rainfall is lowest.

Although the watershed of the lake includes an area of 65,000 km², pollen flux is dominated by input from a smaller source area. Prior taphonomic and pollen transport studies at Lake Malawi have shown that pollen is transported to the north basin through wind or river input and is representative of the vegetation in the northern third of the watershed, about 20,000 km² (DeBusk, 1997). Pollen from grassland and montane taxa are transported preferentially by seasonal winds whose strength varied during the late Pleistocene (Filippi and Talbot, 2005). Today, most wind-transported pollen comes from the north during the austral summer when NE trade winds predominate and the majority of plants flower. However, increased input from the south is possible during times of enhanced SE tradewinds. Tropical seasonal forest, aquatics, and Pteridophytes are preferentially transported by rivers draining the Rungwe Highlands and the Nyika Plateau (Songwe River and South Rukuru River, respectively; Patterson and Kachinjika, 1995; Debusk, 1997).

**Methods**

MAL05–2A was collected in 2005 (Figure 1; 10°1.1’S, 34°11.2’E; 359 m water depth). Coring site, stratigraphy and age model details are provided elsewhere (Brown et al., 2007; Scholz et al., 2007). 40 samples were counted from a 3-m section (6–9 m below lake floor [mbfl]) chosen to bracket the YD interval, consisting mainly of diatomaceous silty clay. The age model of the upper 22 m is based on a second-order polynomial of 24 calibrated AMS 14C dates, four of which fall within our section (Figure 2; calibrated with Fairbanks et al., 2005). We processed 1-cm³ samples using standard methods with the addition of Lycopodium spores and sieved at 10 μm (Faegri and Iversen, 1989). Average resolution between samples is 208 yr but less than 100 yr from 14 to 11 ka. At least 500 grains were counted per sample and no barren samples were observed. Pollen from 215 taxa were identified using the African Pollen Database (APD: http://medias.obs-mip.fr/apd; Vincens et al., 2007b) and atlases of pollen morphology (e.g. Maley, 1970; Bonnefille, 1971a,b; Bonnefille and Rioullet, 1980). Pollen percentages were calculated against a sum of all pollen and spores minus undeterminable grains, aquatics, and Bryophytes, which were calculated separately (Figure 2). Pollen influx rates (grains/cm²/yr) were calculated using the concentration values and sediment accumulation rates. We drew pollen diagrams using Tilia 1.0.1 (Grimm, 1990) and determined zonation by constrained cluster analysis using CONISS (Figure 2; Grimm, 1987). Non-significant variations recorded by the most characteristic taxa were smoothed by the use of five-sample running mean of pollen influx rates (Figure 3c). Pollen taxa assemblages described here are based on biomes outlined by Vincens et al. (2006) for East African vegetation and Debusk (1994; 1998) for Lake Malawi. Tropical seasonal forest and Zambezian woodland are based on the grouping used by Garcin et al. (2007) at Lake Masoko for ease of comparison. A gap in samples exists from 15.5 to 14.7 ka as no sediment remained in this interval after previous sub-sampling and is excluded from the pollen zones. The pollen data is compared with geochemical analyses from this core (Zr:Ti; Brown et al., 2007) and the adjacent, previously studied piston cores from the Malawi north basin (Hydrogen Index [HI], δ¹³C algae, δ¹⁸O diatom-TEX86; Filippi and Talbot, 2005; Powers et al., 2005; Barker et al., 2007; Castañeda et al., 2007).

**Results**

Pollen preservation is excellent throughout and concentrations are high (mean = 25,333 grains/cm³). Abundance of broken/ reworked grains is never more than 4.6% but typically ~1%. Our pollen stratigraphy is divided into three zones based on dominant vegetation assemblages and further subdivided into subzones to illustrate trends in important taxa (Figure 2). Both percentages and influx values for prominent pollen taxa and vegetation assemblages will be described in order to eliminate possible transport artifacts in the percentage data (Figures 2, 3c).

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**Figure 2.** Pollen diagram of MAL05–2A percentages. Pollen sums are all taxa less aquatics, Bryophytes and undeterminable grains, which are calculated separately. Gray curves are exaggerated 5 times. Other Montane grouping includes: Afrocarnia volliensis, Anthocharpum, Dodoneae viscosa-type, Hagenia abyssinica, Ilex mitis, Nuxia/Ficalhoa, Prunus africana-type. Pollen zones are based on constrained cluster analysis (Grimm, 1987). AMS dates that are part of the age model and fall within the section are presented on the right side of the diagram.

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Zone 1: 18.1–15.5 ka

Subzone 1a (18.1–16.4 ka) shows both percentages and influx values dominated by afromontane taxa (Podocarpus, Ericaceae undiff., Juniperus-type, Olea africana-type, Olea capensis-type, Other Montane). These taxa are at their peak values (27%; 450 grains/cm²/yr) and stay relatively stable throughout this subzone. A strong presence of Poaceae (36%; 520 grains/cm²/yr) indicates that grasses were widespread. In addition, aquatic taxa and indicators of shoreline proximity, such as Typha, are at their maximum values (5%; 8.4 grains/cm²/yr) but decline at the top of the subzone. Subzone 1b (16.4–15.5 ka) shows the first major change in the record. Afromontane taxa begin a steady decline (20%; 250 grains/cm²/yr) coincident with the expansion of tropical seasonal forest taxa (3–7%; 20–60 grains/cm²/yr; Macaranga-type, Moraceae, Myrianthus-type holstii, Trema-type orientalis) and Zambezian woodland pioneers (4–7%; 50–75 grains/cm²/yr; Brachystegia, Combretaceae, Uapaca). The first large peak of Urticaceae (1.4%; 19 grains/cm²/yr) occurs at the beginning of this subzone, linked with the expansion of tropical seasonal forest.

Zone 2: 14.7–11.8 ka

Subzone 2a (14.7–13 ka) is marked by abundant grass (45%; 650 grains/cm²/yr). Zambezian woodland percentages show a gradual increase starting at ~14.5 ka. Afromontane abundances continue to decline steadily (19–7%; 250–98 grains/cm²/yr). Tropical seasonal forest (10%; 95 grains/cm²/yr) initially expands but remains at relatively low values. Subzone 2b (13–11.8 ka) brackets the YD interval, and influx values show a two-phase change in vegetation (Figure 3c). The first phase lasts from 13 to 12.3 ka and is characterized by maximum values of tropical seasonal forest (167 grains/cm²/yr) and Urticaceae (26 grains/cm²/yr). A slight increase of afromontane taxa (163–250 grains/cm²/yr) and Pteridophytes (19–65 grains/cm²/yr) is also observed. This increase in both lowland and montane forest taxa is at the expense of Poaceae, which reaches its lowest flux (232 grains/cm²/yr). The second phase, from 12.3 to 11.8 ka, is marked by the decline of all taxa that reached peak values during the first phase in favor of Poaceae (454 grains/cm²/yr).

Zone 3: 11.8–9.5 ka

Subzone 3a (11.8–10.7 ka) is marked by a relatively rapid increase in Poaceae and its highest percentages (54%; 691 grains/cm²/yr). Gradual increases of Zambezian woodland (9–14%; 70–116 grains/cm²/yr) continue during this subzone. Tropical seasonal (13–6%; 98–24 grains/cm²/yr) and afromontane forest (11–2%; 81–17 grains/cm²/yr) percentages decline gradually, and Pteridophytes (~1%; 10 grains/cm²/yr) are nearly absent by the end of the record. Subzone 3b (10.7–9.5 ka) is distinguished by a small increase of Zambezian woodland (14–19%; 116–221 grains/cm²/yr) associated with a larger contribution of Combretaceae.

Interpretation and discussion

Decline of afromontane forest (18.1–15.5 ka)

Afromontane taxa dominated this first period along with indicators of freshwater flow (Figure 3c). Freezing conditions at higher altitudes, cooler lowland temperatures, and lower pCO₂ caused montane taxa to grow at a lower elevation than present allowing for closer proximity to the lakeshore (Jolly and Haxeltine, 1997; Street-Perrott et al., 1997; Wu et al., 2007). Previous pollen-derived estimates of last glacial maximum (LGM) temperature in East Africa suggested that the lower montane forest limit descended to 600–900 m asl (relative to ~1500 m asl modern; Coetzee, 1967; Livingstone, 1967; Debusk, 1994). However, low Podocarpus percentages (~5%) at Lake Masoko (840 m asl) suggest that the limit was near but still above this elevation (Vincens et al., 2007a). As Masoko receives no fluvially transported pollen, this percentage indicates that montane forests grew within 25 km, based on studies of aerial transport of Podocarpus grains (Vincens, 1983). Thus, montane forest likely grew at the upper end or even above the altitude suggested by earlier estimates. Our placement of the lower montane forest limit near 900 m asl, rather than as low as 600 m asl, is consistent with more recent TEX₈⁶g from Lake Malawi yielding a ~3.5°C temperature anomaly relative to modern for this period, much less than the previous pollen-derived estimates.

Close proximity of Masoko and Malawi ensures that the wind-transported montane fraction in both lakes is largely similar, thus the difference at Malawi represents the fluvial contribution ranging from 15 to 35%. Due in part to anthropogenic forest clearance, modern afromontane vegetation occurs in discontinuous patches of forest surrounded by extensive high-altitude grasslands (White, 1983). As a result, these afromontane pollen taxa in modern sediments from the north basin never exceed 14% (Debusk, 1997); however, soil samples from within the forest range from 26 to 30% (Vincens et al., 2006). Similar high values in Malawi sediments from 18.1 to 14.7 ka (Figure 2; 20–40% of which ~15–35% is via rivers) imply a compositional change of upper watershed vegetation such that afromontane forests were more extensive and less fragmented than present. A reduction of montane grasslands relative to today is also supported by δ¹³C cant from Malawi, a record of C₄/C₃ abundance from plant leaf waxes, suggesting predominantly C₃ inputs at the very beginning of this record (Figure 3a; Cañeteda et al., 2007). This implies lowland grass input, possibly from the Songwe River alluvial plain (Livingstone and Clayton, 1980).

During the gradual decline of afromontane taxa at Malawi, lowland forest and woodland pioneers begin to increase between 17 and 16 ka (Figure 3c). At the same time, a dramatic rise of moister montane taxa (mainly Olea capensis-type) is observed at Lake Masoko but not accompanied by an increase of Zambezian woodland. This suggests that the establishment of woodland was gradual throughout the Malawi watershed. This transition reflects rising temperature (~1°C/ka) and episodic wetting (McClue et al., 2008; Powers et al., 2005; Barker et al., 2007). This is consistent with declining C₃ input to the core site (~5%; Cañeteda et al., 2007) as well as continued retreat of the afromontane belt (Figure 3).

Interestingly, subzone 1b (16.4–15.5 ka; Figure 2) is roughly coincident with the timing of Heinrich Event 1 (H1; Hemming, 2004). However, rather than the abrupt cooling and aridity recorded elsewhere in Africa and the tropics (Stager et al., 2011), this zone is instead defined by gradual increases in both lowland vegetation types (Zambezian woodland and tropical seasonal forest). Similar trends are also observed at Lakes Tanganyika and Rukwa, implying that this is a regional vegetation change likely related to the slow temperature increase seen in the TEX₈⁶g record (Figure 3a; Vincens, 1991, 1993; Vincens et al., 2005; Powers et al., 2005). One exception is Olea africana-type, the only component of the drier montane forest
which increases at the time of H1; however, this is possibly a pioneer response to the decline in other montane forest taxa.

Expansion of lowland forest (14.7–13 ka)

The progressive warming following the LGM corresponds with continued retreat of afromontane taxa to high-altitudes recorded in both records at Malawi and Masoko. This opening provoked a reorganization of the lowland vegetation that had been dominated by afro-

montane forests and grasslands. The increase in both drought-
tolerant woodland (Zambezian woodland) and drought-intolerant forest (tropical seasonal forest) suggests that vegetation was more heterogeneous and forests more prevalent than present. However, the stronger woodland presence until 13.8 ka suggests that the dry season must have been severe enough to limit dense forest at least locally. Drought-intolerant forest assemblages preferentially established along rivers that would have received enhanced runoff from the northern highlands (Johnson and Ng'ang'a, 1990).

Increases of grass during this zone could derive from high- or low-

land sources; however, decreased grass percentages at Lake Masoko suggest that lowland grasses were actually less prevalent (Vincens et al., 2007a). Instead, the expansion of high-altitude grasslands, previously limited by afro-montane forest, likely accounts for the regional increase in grass. This is supported by depleted δ13C values implying greater C3 plants contribution (Figure 3a; Castañeda et al., 2007); however this may also be partially related to the increases in arboreal taxa described above.

Though there is evidence of early post-glacial warming in south-
east Africa (Powers et al., 2005; Tierney et al., 2008), significant increases in moisture are not observed until ~14.5 ka associated with warming in the Northern Hemisphere (NH) high-latitudes (Barker et al., 2007; Castañeda et al., 2007). Higher effective moisture and enhanced riverine transport at this time is reflected by the gradual increase of tropical seasonal forest, shade-dwelling herbs typical of forest undergrowth (Urticaceae), and ferns (Pteridophytes) beginning at 14.7 ka (Figure 3c). This conclusion is also supported by stable isotopic analyses, which trend toward more depleted values coeval with the shift to moister lowland forest vegetation (Figure 3a; Barker et al., 2007; Castañeda et al., 2007).

At 13.8 ka, grass and most herbaceous taxa return to lower abundances until after 11.8 ka; however, tropical seasonal forest continues increasing. At Lake Masoko, an abrupt transition from moister montane forests to tropical seasonal forest also occurs at this time (Vincens et al., 2007a). Though δ18O values from Malawi suggest higher MAP, for further expansion of drought-intolerant taxa, very low dry season severity would have also been necessary (Figure 3; Barker et al., 2007; Tierney et al., 2008). High HI values, indicating algal organic matter inputs consistent with greater north basin upwelling, suggest that this was a period of weakened SE tradewinds (Figure 3b; Filippi and Talbot, 2005). This, in addition to a 2°C cooling at Malawi, probably resulted in higher effective moisture and decreased evaporative stress during the dry season (Figure 3a; Powers et al., 2005).

Records from both equatorial east African (EEA; 4°N–6°S; discussed here: Lakes Malawi, Tanganyika, Rukwa, and Masoko) and southeast African (SEA; 6°S–14°S; discussed here: Lakes Emakat and Victoria and Rusaka Swamp) show similar vegetation trends until ~13 ka (Figure 1). As at Malawi and Masoko, records from Lakes Tanganyika (8°30’S) and Rukwa (8°25’S) also show a decline of afromontane forest taxa followed by an increase in tropical seasonal forest around 14.5 ka (Figure 4; Vincens, 1989, 1991, 1993; Vincens et al., 2005; Vincens et al., 2007a). In EEA, moist Hogirania forest became prevalent in the highlands near Lake Emakat (2°55’S) and Rusaka Swamp (3°26’S). Lack of moister forest at Lake Victoria (0°34.5’S) until after 11.5 ka suggests that lowland conditions were less favorable to forest establishment (Bonneille et al., 1995; Beuning, 1997; Ryner et al., 2006).

Two-phase vegetation change at the YD (13–11.8 ka)

During the YD, two different assemblages occur in the watershed from 13 to 12.3 ka and 12.3 to 11.8 ka. The first assemblage shows small increases in afromontane taxa that reflect cooler, drier conditions and steady increases in tropical seasonal forest, implying a continued lack of a long dry season (Figure 3c). It is unlikely that the increases in montane forest resulted from enhanced wind transport from stronger NE tradewinds, which are relatively weak during this first phase in relation to the second phase (Figure 3b; Brown et al., 2007). Although this does not seem to indicate a lowering of the afro-

tendance belt to LGM altitudes, it is most likely that the 2°C cooling recorded at Malawi allowed these assemblages a temporary reestablishment at lower altitudes than today (Powers et al., 2005). Increased values of river transported taxa such as Pteridophytes also increase coeval with tropical seasonal forest; however, Barker et al. (2007) record this as period of low river input to the basin. High values of this taxon during a time of reduced river input instead are likely a result of forest expansion due to the strong presence of ferns associated with dense forest (White, 1983).

The second assemblage shows a recovery of grass at the expense of montane and lowland forest taxa (Figure 3c). In addition, taxa associated with dense forest, such as Urticaceae and Pteridophytes, show a similar decline. Maintenance of Zambezian woodlands suggests that although high and lowland forests were replaced by grassland, drier woodlands were unaffected.

Interpreting these finely resolved vegetation phases requires a small subsampling interval and good age control. This subzone includes an AMS date at 12,067±157 cal ka BP with small error (10,577±13°C yr BP), and assemblages are based on eight samples (Figure 2; Brown et al., 2007). Given this control and the internal consistency in results between adjacent samples, we feel confident in these phases despite their short duration.

Similar to Malawi, regional maintenance of tropical seasonal forest also occurred at Lake Masoko; however, woodland behaved differently between the two sites (Figure 4; Vincens et al., 2007a). Uapaca, a drought-tolerant pioneer species, underwent no abrupt change in either direction during the YD at Malawi. In contrast, at Masoko, no presence of woodland is recorded until after the YD. Strong woodland abundance regionally at Malawi, but not locally at Masoko, suggests that from 13 to 12.3 ka, the denser tropical seasonal forest was growing exclusively in areas of edaphically moister conditions. Zambezian woodland was extensive in the better drained, less sheltered locations. Stable Zambezian woodland influx values suggest that idea that increased tropical seasonal forest at both Masoko and Malawi, under 12.3 ka and 11.7 ka, respectively, do not indicate higher MAP (Figure 4; Barker et al., 2007; Tierney et al., 2008). This is consistent with indications of aridity after 13 ka at Lake Malawi and throughout the African tropics (Gasse, 2000; Barker et al., 2007). With modern rainfall seasonality, an expansion of grasslands or dry woodland would be expected given lower rainfall (Hely et al., 2006). It is likely that decreased dry season severity is responsible for controlling higher local effective moisture at more sheltered localities, like Lake Masoko, within the Malawi catchment.

During cold phases in the NH, the ITCZ is displaced southward and can be narrower (Haug et al., 2001; Lea et al., 2003). An ITCZ excursi-

on into southeast Africa has been used to explain higher relative moisture in parts of this region (Finney and Johnson, 1991; Garcin et al., 2007) as well as summer rainfall as far south as 26–30°S (Van Zinderen Bakker and Butzer, 1973). However, the LGM, H1, and YD, no increase in moisture is recorded at Lake Malawi (Barker et al., 2007; Brown et al., 2007; Castañeda et al., 2007). Tierney et al. (2008) have suggested that the effect of ITCZ position on regional
hydrology is secondary to other controls, such as moisture advection and monsoon strength. Due to decreases in Indian and Atlantic SSTs during the YD, reduced latent heat flux and weak moisture advection to the continent are in agreement with other indications of reduced MAP (Sonzogni et al., 1998; Schefuß et al., 2005).

Zr:Ti ratios from the MAL05-2A core, recording volcanoclastic input from the Rungwe Highlands north of the core site rich in Zr, date the beginning of stronger NE trades to ~12.7 ka (Figure 3b; Brown et al., 2007). This suggests a southward ITCZ over Malawi acted to even out rainfall seasonality. In addition, a second 2°C temperature decrease at the beginning of this interval coupled with weaker SE tradewinds, indicated by HI, would have reduced evapotranspiration during the dry season (Figure 3b; Filippi and Talbot, 2005; Powers et al., 2005; Schefuß et al., 2005). In summary, despite lower MAP, the resulting change in rainfall seasonality and weak winds created edaphically favorable conditions along rivers and in areas receiving runoff from the highlands, thereby allowing the persistence of drought-intolerant taxa until ~12.3 ka.

The impact of effective moisture on vegetation assemblages during the YD controlled by temperature, tradewind strength, and rainfall seasonality is further illustrated during the second vegetation phase (Figure 3; 12.3–11.8 ka). After the peak of tropical seasonal forest and Pteridophytes at the end of the first vegetation phase, both assemblages began to decline gradually. The opposite is observed in the grasses, which increased until the end of the record.

The decline of the drought-intolerant forest must have been caused by one of three controls: an increase in rainfall seasonality, a further decrease in MAP, or higher evaporative stress. A rainfall seasonality change seems unlikely, as records of aridity in northern Africa and relatively moister condition in South Africa suggest that the ITCZ remained in a southerly position throughout both vegetation phases (13–11.8 ka; Van Zinderen Bakker and Butzer, 1973; Gasse, 2000). An even further decline in MAP is also not likely given relatively stable values of δ18Odiatom throughout the second phase (Figure 3a; Barker et al., 2007).

The most dramatic climatic change at this time is the maximum NE tradewinds intensification from ~12.3–11.8 ka (Figure 3; Brown et al., 2007; Talbot et al., 2007). It seems likely that further evaporative stress caused by stronger austral summer trades could have initiated the degradation of the drought-intolerant forest. Stronger evaporation could also explain the slight changes in the isotopic records without any further change in MAP (Figure 3a).

We propose that from 13 to 12.3 ka, a more southerly ITCZ coupled with cooler temperatures reduced dry season severity at Lake Malawi. This change allowed drought-intolerant tropical seasonal forest to flourish despite reduced MAP. From 12.3 to 11.8 ka, enhanced NE tradewinds promoted slow, progressive drying of the watershed. The increased evaporative stress, coupled with low MAP, caused a gradual retreat of tropical seasonal forest as local edaphically moist areas, such as Lake Masoko, passed critical thresholds and became rarer while runoff and river input simultaneously decreased.

From ~13 to 11.8 ka in East Africa, a complicated pattern developed that illustrates the effects of a southward ITCZ and reduced MAP throughout the region (Gasse, 2000). In EEA, moist forest development was interrupted at ~13 ka, and grasslands expanded until

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**Figure 4.** A) Pollen percentages of drought-intolerant tropical seasonal forest from 16.5 to 9 ka for sites in southeast Africa (Vincens, 1991, 1993; Vincens et al., 2005, 2007a). Bottom panel is Zr:Ti from the north basin of Lake Malawi (Brown et al., 2007). Gray box marked ‘NE’ represents northeast tradewind reinforcement. B) Pollen percentages of drought-tolerant Zambezian woodland from 16.5 to 9 ka for sites in southeast Africa (Vincens, 1991, 1993; Vincens et al., 2005, 2007a). Bottom panel is Hydrogen Index (HI) from the north basin of Lake Malawi (Filippi and Talbot, 2005). Gray boxes marked ‘SE’ represents southeast tradewind reinforcement.
11.5 ka when moister vegetation types returned during the Early Holocene (Bonnefille et al., 1995; Beuning, 1997; Ryner et al., 2006). In contrast, in SEA, woodland and tropical seasonal forest continued to develop until −11.8 ka (Figure 4; Vincens et al., 2005, 2007a). Two core records from the extreme north and south ends of Lake Tanganyika highlight the different regional responses. In Tanganyika’s north basin (4°30′S), grassland expansion during the YD is similar to the pattern in EEA, while the south basin (8°30′S) experienced a transition to Zambezian woodland after the YD as seen in SEA (Vincens, 1991, 1993).

Though drought-intolerant species dominated locally at Lake Masoko until 11.7 ka, records from southern Lake Tanganyika and at Lakes Rukwa and Malawi suggests the importance of both drought-tolerant and intolerant vegetation types in SEA. On a regional scale, Zambezian woodland and grasslands were widespread after −14.5 ka, long before the abrupt post-YD succession to dry woodland at Masoko. The later response at Masoko is probably due to hydrological buffering by groundwater (Barker et al., 2003). The gradual regional decline of forest at Lake Malawi signifies that a shorter dry season allowed some areas in the watershed to remain sufficiently moist to sustain forest until the 11.7 ka termination at Lake Masoko, when establishment of the driest conditions occurred.

Two regions of spatially coherent vegetation responses occur north and south of −6°S despite uniform MAP decreases. A rainfall regime in SEA similar to what is observed today in EEA, with a bimodal pattern rather than a long, dry season and single rainy season, likely occurred. (Figure 5; Garcin et al., 2006, 2007; Vincens et al., 2007a). The deterioration of moist forest in EEA during the YD implies a opposite change in rainfall repartition resulting in a longer dry season exacerbated by decreased MAP. The increase of grassland highlights the dependence of EEA moist forest vegetation on the twice-yearly ITCZ passage.

Rise of woodland/grassland (11.8–9.5 ka)

A substantial increase of grass occurred at Lake Malawi during the early Holocene around 11.8 ka (Figure 3c). This important change represents an opening of the vegetation that followed the progressive decline of tropical seasonal forest, Urticaceae, and Pteridophytes. At Lake Masoko, the local, lowland vegetation change was more abrupt and coincident with the reorganization of dominant surface winds over the lake (Figure 4; Filippi and Talbot, 2005).

The reinforcement of the dry season SE tradewinds, as indicated by low HI values (Figure 3b), marked the beginning of a −100 m lowstand at Malawi from 11.8 to 10.3 ka, out of phase with other East African lakes (Gasse, 2000; Johnson et al., 2002; Barker et al., 2007). Higher rainfall north of 9°S at the beginning of the humid Early Holocene (DeMenocal et al., 2000; Tierney et al., 2008), suggests that the ITCZ was displaced northward in response to insolation and high-latitude forcing. This extended the length of the dry season over southeast Africa, exacerbated by greater wind stress (Figure 3b; Filippi and Talbot, 2005; Tierney and Russell, 2007).

These conditions would have favored more drought-tolerant taxa like C4 grasses, Uapaca, and Combretaceae, a drier woodland taxon that increases around 10.7 ka. Though C4 plant input began to increase during this period, it is likely that the expanding lowland grasses were predominantly C4 (Castañeda et al., 2007). The slow decrease in δ13Calk is explained by increased C3 arboreal woodland taxa in the lowland as well as an expansion of montane grasslands, as afro-montane forests reached their lowest abundance of the record (Figure 3).

Zambezian woodland diversified during the Early Holocene throughout East Africa (Bonnefille et al., 1995; Ryner et al., 2006; Vincens et al., 2007a). At Malawi, δ18Owater and δ13Calk values became more depleted indicating higher MAP around 10.3 ka; however, the tropical seasonal forest which characterized the deglacial interval did not recover (Figure 3; Barker et al., 2007; Castañeda et al., 2007). The success of Zambezian woodland relative to tropical seasonal forest in the Early Holocene supports the ideas that dry season length rather than MAP is limiting to the later biome. Collins et al. (2011) have suggested that changes in ITCZ width rather than mean position may not have been responsible for aridity in the tropics during northern hemisphere cold periods; however, this cannot explain the change in rainfall seasonality observed over SEA during the last deglaciation.

Figure 5. A) Modern latitudinal extent of summer unimodal and bimodal rainfall zones in tropical Africa. B) Pollen-inferred latitudinal extent of summer unimodal and bimodal rainfall zones in tropical Africa during pollen subzone 2b from ~13 to 11.8 ka.

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Conclusions

Our vegetation record shows a regional signal of high montane taxa abundances that diminish following the LGM. We suggest a lowering of the tree-line to ~900 m asl, less than previously proposed. In addition, an expanded arbooreal component of the afro montane biome occurred.

This study highlights the importance of local conditions and rainfall seasonality in maintaining vegetation. Tropical seasonal forest began to increase at 14.5 ka and continued to expand in SEA during the first part of the YD. Despite regional aridity, drought-intolerant assemblages were maintained because of reduced evaporative stress, which allowed for moister edaphic conditions in parts of the watershed. From 12.3 to 11.8 ka, a reinforcement of the NE trade-winds caused a slow opening of the lowland vegetation and replacement of drought-intolerant tropical seasonal forest by grassland and woodland.

The local signal at Lake Masoko compared with the Malawi regional signal supports the notion that drought-intolerant vegetation persisted in the midst of aridity as a result of optimal geographic location. These records suggest decreased rainfall seasonality and dry season severity from ~14.5 to 11.8 ka. Our record shows that whereas reductions in rainfall and evaporative stress from intense winds caused a gradual forest decline beginning at ~12.3 ka affecting well-drained areas, the change in rainfall seasonality at 11.8 ka to more modern long dry season resulted in a rapid conversion from forest to woodland of even relatively buffered moist edaphic locations.

The YD in SEA illustrates that although rainfall is a primary control on vegetation distribution, other factors, such as wind, temperature, and local setting, all contribute to overall effective moisture on the landscape and cannot be ignored. Clearly, the interpretation of palynological records, as well as predictions of future vegetation changes, should be viewed in terms of a complex system rather than simple physiological responses to temperature or MAP. In addition, the comparison of local versus regional records helps us to discern environmental responses to regional and local hydrologic thresholds.

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