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Influence of topography on tropical African vegetation coverage

Gerlinde Jung[1] · Matthias Prange[1,2] · Michael Schulz[1,2]

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Abstract Hominid evolution in the late Miocene has long been hypothesized to be linked to the retreat of the tropical rainforest in Africa. One cause for the climatic and vegetation change often considered was uplift of Africa, but also uplift of the Himalaya and the Tibetan Plateau was suggested to have impacted rainfall distribution over Africa. Recent proxy data suggest that in East Africa open grassland habitats were available to the common ancestors of hominins and apes long before their divergence and do not find evidence for a closed rainforest in the late Miocene. We used the coupled global general circulation model CCSM3 including an interactively coupled dynamic vegetation module to investigate the impact of topography on African hydro-climate and vegetation. We performed sensitivity experiments altering elevations of the Himalaya and the Tibetan Plateau as well as of East and Southern Africa. The simulations confirm the dominant impact of African topography for climate and vegetation development of the African tropics. Only a weak influence of prescribed Asian uplift on African climate could be detected. The model simulations show that rainforest coverage of Central Africa is strongly determined by the presence of elevated African topography. In East Africa, despite wetter conditions with lowered African topography, the conditions were not favorable enough to maintain a closed rainforest. A discussion of the results with respect to other model studies indicates a minor importance of vegetation–atmosphere or ocean–atmosphere feedbacks and a large dependence of the simulated vegetation response on the land surface/vegetation model.

Keywords Global climate modelling · African vegetation · Topography · Paleoclimate · Late Miocene

✉ Gerlinde Jung
gjung@marum.de

[1] MARUM - Center for Marine Environmental Sciences, University of Bremen, 28334 Bremen, Germany

[2] Faculty of Geosciences, University of Bremen, 28334 Bremen, Germany

1 Introduction

The development of upright walking hominids in late Miocene East Africa has been attributed to an environmental change from a densely forested environment to a more open grassland habitat (e.g. Cerling et al. 2011). Against that background, the co-occurrence of important steps in hominid evolution with consecutive drying and major shifts in vegetation coverage from C_3 dominated ecosystems to C_4 dominated grasslands, especially in East Africa, was discussed (Cerling et al. 1997). In parallel climatic conditions and vegetation coverage changed in the tropical region of Central Africa throughout the Neogene (Senut et al. 2009). Here we first review the climate regime in Africa and its related vegetation at present day, as well as the development in the past. We hypothesize that late Neogene tectonic uplift had an important impact on the hydro-climatic conditions and consequently also on vegetation in the African rainbelt. To test this hypothesis we performed model sensitivity experiments, altering the topography of Africa, as well as the Himalaya and the Tibetan Plateau. This is, to our knowledge, the first study on the effect of mountain uplift in both regions that uses a comprehensive atmosphere–ocean general circulation model (GCM) at fine spatial resolution coupled to a dynamic vegetation model allowing for the simulation of climate–vegetation feedbacks and atmosphere–ocean interactions. The relatively high resolution helps to represent mountain elevations much more realistically than with coarsely resolved models.

2 Climate, vegetation and mountain uplift

2.1 Present day vegetation and climate of Africa

At present day, humid climate favours dense rainforests over large areas of Central Africa, and in a smaller block in West Africa, whereas East Africa is characterized by Savannah type open grassland habitats (Plana 2004; Salzmann et al. 2009) with only limited patches of rainforest (Couvreur et al. 2008).

The tropical rainbelt in Africa is characterized by a strong precipitation regime over Central Africa, with two distinct rainy seasons (Pokam et al. 2012) and a regionally diverse pattern of rainfall seasonality over East Africa (Nicholson 1996). The seasonality in Northern Africa is strongly determined by the intra-annual movement of the Intertropical Convergence Zone (ITCZ) that separates the moist monsoonal inflow from the Atlantic Ocean from dry north-eastern trades (Nicholson 2000). At higher altitudes the precipitation regime is influenced by the mid-tropospheric African Easterly Jet (AEJ) which plays a role in moisture and energy supply for atmospheric disturbances (Cook 1999; Wu et al. 2009b) and the upper level Tropical Easterly Jet. The Tropical Easterly Jet forms as a consequence of the heat low over the Tibetan Plateau and also impacts the development of disturbances in the zonal flow of the AEJ (Hulme and Tosdevin 1989). In East Africa the Somali or Findlater Jet which is the cross-equatorial flow at the southern edge of the monsoon trough and channelled by the East African topography, influences moisture transport to the Indian monsoon region (Findlate 1969; Slingo et al. 2005; Vizy and Cook 2003). In Southern Africa the position of the Congo Air Boundary separates air masses coming from the Indian Ocean and the westerly flow of Atlantic origin (Nicholson 2000).

The distribution of rainfall in tropical Africa is strongly altered by regional topography. The East African rift system with its plateaus and mountains acts in many ways on the rainfall regime of the region: it supports convective heating, enhances convection through orographically forced lifting of air, and alters regional precipitation patterns by lee and luv effects due to blocking or channelling of the low-level flow (Levin et al. 2009). Therefore, most of the moisture from the Indian Ocean is rained out on the way, when it is lifted over the Southern and Eastern African Plateaus (Meehl 1992), while most of the moist Congo air is blocked by the East African Rift and does not reach the coastal zone of East Africa (Nicholson 1996).

2.2 Tropical African vegetation and climate development

By the mid-Miocene rainforests extended from the West to the East coast over tropical Africa (Coetzee 1993; Plana 2004). East African proxy records show a shift towards a C_4 based diet in grazers from 8.5 Ma ago (Jacobs 2004), which has been widely interpreted as shift from forest coverage to grassland environments. However, recent studies on vegetation development of the last 10 Ma indicate the absence of a closed forest belt in tropical Africa during that entire time span (Bonnefille 2010). The increase in C_4 plants during that time period (Brown et al. 2011; Cerling 1992; Edwards et al. 2010) might also be disconnected from an increase in grassland, but rather indicating a replacement of a similar, but C_3 dominated ecosystem (Feakins et al. 2013).

On a global scale a drying and cooling trend from the mid to late Miocene was detected. This trend was suggested to have been induced by a changing atmospheric CO_2 concentration (Pound et al. 2012). Additional processes that might have likely influenced African long-term climate evolution in the Neogene are, amongst others, the restriction of the Indonesian Seaway and the closing of the Tethys Ocean and shrinkage of the Paratethys. The shrinkage of the Tethys started in the late Oligocene and was a rather continuous process that probably lead to a drying of East, North and Central Africa (Zhang et al. 2014). The restriction of the Indonesian throughflow in the Pliocene has been suggested to have led to a cooling of the central Indian Ocean and due to the link between Indian Ocean sea surface temperature and East African rainfall also to a drying of Eastern Africa (Cane and Molnar 2001). Mountain uplift was also suggested to have played a role in African climate evolution. Asian uplift was discussed to have strengthened the cross-equatorial flow of the Somali Jet along the East African coast that transports moisture to the Indian subcontinent (Chakraborty et al. 2002; Fluteau et al. 1999). Also Neogene uplift of the African continent might have caused drying and vegetation changes especially over Eastern Africa as suggested by various model experiments (Kaspar et al. 2010; Prömmel et al. 2013; Sepulchre et al. 2006; Slingo et al. 2005; Sommerfeld et al. 2014).

Superimposed on that secular drying trend, climate variability on shorter time scales is also evident in proxy records. Some proxy studies indicate variable climate and vegetation conditions both geographically and through time (Kingston 2007) with periodically occurring and intensifying arid periods since the late Miocene (Maslin et al. 2014). The diversification of rainforest trees in East Africa and the origins of endemic species was also found to have occurred stepwise, during times of repeated isolation and reconnection between West/Central and East African rainforests prior to the Pleistocene (Couvreur et al. 2008). Moreover arid and humid conditions varied largely through time and space in Central Africa during the Neogene. In the Congo basin, thick mid-Miocene sand deposits indicate semi-arid conditions in today's humid tropical region (Senut et al. 2009). One late Miocene period that might have been characterized by some variation also in African climate is the Messinian Salinity Crisis. According to (Schneck et al. 2010) in phases of repeated isolation of the Mediterranean from the Atlantic Ocean that led to a drying of the Mediterranean Sea West and Northern Central Africa were characterized by a precipitation increase due to higher moisture transports from the Atlantic into the region. Rapid fluctuations in vegetation coverage and climate during the Pliocene and Pleistocene are most likely related to global changes forced by orbital configuration and the intensification of northern hemisphere glaciation (Kingston 2007; Leroy and Dupont 1994). According to Ruddiman et al. (1989) mountain uplift could well have served to potentially amplify the effects of this orbitally triggered climatic variability.

2.3 Asian and African uplift history

The timing of uplift and estimates of uplift rates in Africa, as well as in the Himalaya/Tibetan Plateau region are still under debate. Southern and Eastern African Plateaus are considered to form part of the so-called African superswell (Nyblade and Robinson 1994) that was emplaced in the early Miocene (Seranne and Anka 2005) and successively lifted during the Neogene (Moucha and Forte 2011; Pik 2011). In addition rifting and volcanism formed the landscape of East Africa (MacGregor 2015; Pik 2011). Phases of major uplift in the east African rift system as well as in Southern and South-western Africa occurred from the late Miocene to the Pleistocene (Chorowicz 2005; MacGregor 2015; Roberts and White 2010).

Despite a large scientific interest in Asian monsoon development which is strongly linked to the high plateau of Tibet and the barrier of the Himalaya mountains (Boos and Kuang 2010), uplift history and paleo-elevation of the Himalaya and the Tibetan Plateau are still only weakly constrained (Tapponnier et al. 2001). Suggested uplift histories of the Tibetan Plateau range from a gradual rise since the early Eocene (Garzione et al. 2000; Tapponnier et al. 2001) to a significant increase in altitude in the late Miocene (Raymo and Ruddiman 1992; Turner et al. 1996; Zhisheng et al. 2001) and a rapid late Pliocene–Pleistocene uplift (Ding et al. 1999; Qiang et al. 2001). On the other hand it has also been suggested that the plateau was already at high mean elevation similar to present day before the late Miocene (Coleman and Hodges 1995) and that no significant change in the elevation of the southern plateau can be found since the mid-Miocene (Harris 2006). A recent study demonstrates even the existence of an Andean-type mountain range along the southern margin of the Asian block before the collision of India with Asia during the early Cenozoic (Ding et al. 2014). Despite this controversy there is strong evidence that most likely substantial uplift occurred in most parts of the Tibetan Plateau and the Himalaya since the mid-Miocene and hence an impact on global and regional climate during the Neogene is very likely.

3 Methods

In the present study we use a coupled ocean–atmosphere GCM including a dynamic vegetation module to investigate the impact of topography on climatic conditions and vegetation coverage in tropical Africa. Hence with these simulations the feedbacks between atmosphere and ocean, as well as between vegetation and atmosphere are considered. Several model experiments were performed altering topography of the African–Asian monsoon region (East/Southern Africa and Himalaya/Tibetan Plateau).

3.1 Model description

The simulations were performed with the National Center for Atmospheric Research Community Climate System Model Version 3 (CCSM3; Collins et al. 2006). The model is run in a fully coupled mode, including the four components atmosphere, land, ocean, and sea ice. The atmospheric component (CAM3) and the land surface model (CLM3) are run with a horizontal resolution of ~1.4° (T85); the atmosphere is discretized with 26 vertical layers. The ocean (POP) and sea-ice models (CSIM) are run with a variable grid resolution of 1.125° in zonal direction and roughly 0.5° in meridional direction, with a refinement down to 0.3° towards the equator. The ocean model uses 40 levels in the vertical.

The land model includes a dynamic global vegetation model (DGVM) (Bonan et al. 2003; Levis et al. 2004). This approach allows not only for the direct simulation of vegetation coverage response to climatic conditions, but also takes biogeophysical feedbacks between climate and vegetation into account. The DGVM is based on the Lund–Potsdam–Jena model (Sitch et al. 2003). Vegetation is represented by 10 different plant functional types (PFTs), allocating a distinct area within the grid cell to each PFT (3 grass PFTs, 7 tree PFTs). Leaf area index, canopy height and fractional coverage of the grid cell are determined from the carbon stored in the plants. Calculated net primary production serves as main input for the slow processes in the DGVM. These processes occur in the following order: reproduction, turnover, mortality, allocation, competition for light, background and stress mortality, mortality due to

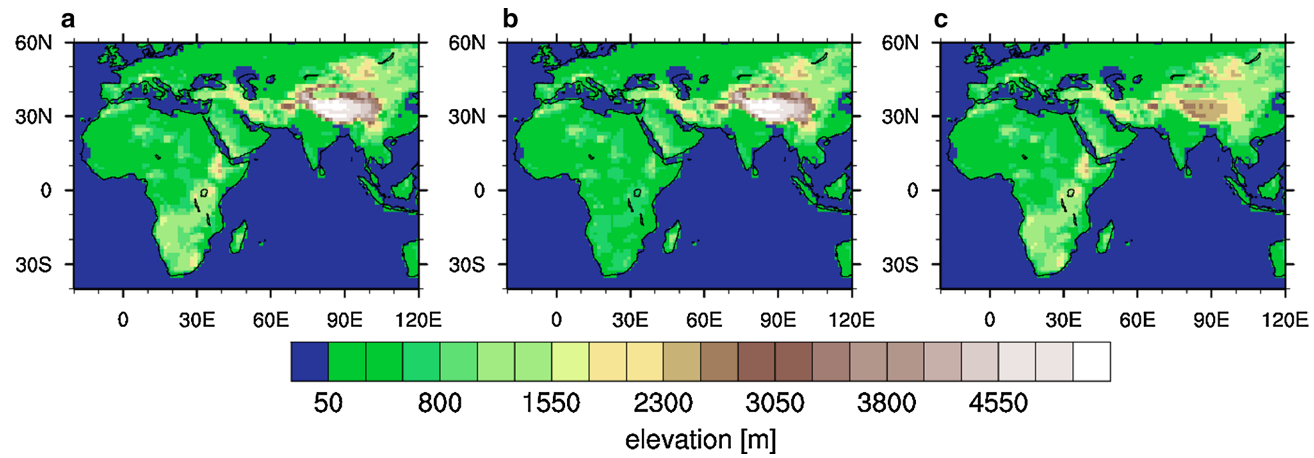

Fig. 1 Model elevations of the different experiments. Present day topography (CTRL) (**a**), South and East African topography 50 % of CTRL (AF) (**b**), Himalaya and Tibetan Plateau topography 50 % of CTRL (HT) (**c**)

fire and establishment. Phenology is calculated every day and vegetation coverage is updated on a yearly basis. The used model setup is capable of taking the biogeophysical vegetation–climate feedback into account (Rachmayani et al. 2015), whereas, due to prescribed atmospheric CO_2 concentrations no biogeochemical feedback is accounted for.

It was discussed that CLM3-DGVM generally overestimates grasslands and underestimates tree coverage (Bonan and Levis 2006) which is consistent with studies that found CLM3 soils to be too dry (Oleson et al. 2008). In order to improve the simulation of vegetation cover, new parameterizations for canopy interception and soil evaporation have been implemented into the land component following Oleson et al. (2008), as in Handiani et al. (2013). For the African environment a precipitation deficit is found in the region of southern Cameroon and Gabon (Chang et al. 2007; Deser et al. 2006) where hence no rainforest can exist. However, over the large areas of Central to East Africa and also in West Africa the model shows a sufficiently good performance in the simulation of present-day potential vegetation cover (Bonan and Levis 2006). Therefore we consider the model suitable for this study.

Some limitations of the use of DGVMs in deep-time paleo-research (Shellito and Sloan 2006) still have to be kept in mind. Parameters are generally tuned to present-day climate and vegetation conditions. Furthermore no nutrient limitation (Hungate et al. 2003) is included. Additionally, in the DGVM no evolution or adaptation of plant species has been accounted for, which, as a continuous process, may be important when longer time spans with changing environmental conditions are considered (Lammertsma et al. 2011). This particularly holds true for the development and spread of the C4 plants.

3.2 Experimental design

Three model experiments were performed. A control simulation (CTRL), as described in detail further below, was run using present-day topography. Two sensitivity studies were performed that are identical to CTRL, except that topography was lowered to half of the present-day altitude in one experiment for Eastern and Southern Africa (AF) as in Jung et al. (2014) and for the Himalaya and the Tibetan Plateau (HT) in the other simulation (Fig. 1). Due to the lack of precise paleo-elevation data and against the background that there is also evidence for some uplift of both regions well before the mid-Miocene we consider a 50 % reduction in topography with respect to present-day suitable for these sensitivity experiments. We would like to stress that with our model experiments we aim at understanding the role of African and Asian topography in tropical African climate and vegetation dynamics rather than trying to reproduce a specific time span of Earth's history. Therefore in these sensitivity experiments topography is the only boundary condition that is changed, to enable an isolated view on the effect that mountains have on climate and vegetation in Africa.

The boundary conditions for the control run (CTRL) include modern geography and topography as well as pre-industrial concentrations of greenhouse gases, ozone, sulphate and carbonaceous aerosols, following the guidelines for pre-industrial simulations formulated by the Paleoclimate Modeling Intercomparison Project, Phase 2 (Braconnot et al. 2007). Assuming pre-desert conditions, the effect of dust aerosols on radiative transfer was set to zero and soil texture and colour were adapted to represent loam in the Sahara. To avoid extreme insolation forcing, the orbital parameters were

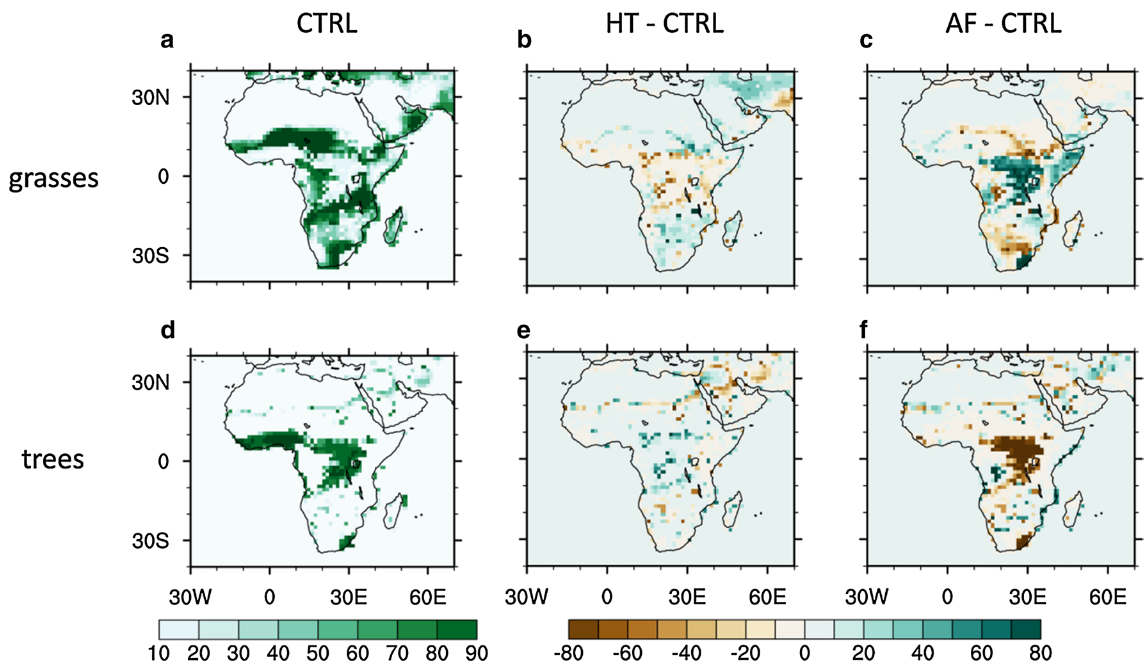

Fig. 2 Percentage coverage with grass and shrub type PFTs for CTRL (**a**) and response to a lowering of model topography in Himalaya/Tibetan Plateau (**b**) and East and Southern Africa (**c**); percentage coverage with tree type PFTs for CTRL (**d**) and response to a lowering of model topography in Himalaya/Tibetan Plateau (**e**) and East and Southern Africa (**f**)

changed to represent average values over a longer period (2–10 Ma) with an eccentricity of 0.027 and an obliquity of 23.25°. The perihelion was set to boreal autumn (359.47°). Compared to a pure preindustrial run that was also performed, our control simulation is characterized by stronger (weaker) insolation in the northern hemisphere in summer (winter) which leads to an increase in seasonality, most pronounced in the northern hemisphere (not illustrated).

The control run was started from a spun-up preindustrial simulation of 500 years obtained from the National Center for Atmospheric Research and run for another 600 years. The experiments were branched off from the control run at year 301 and run for another 300 years. It was demonstrated by Jung et al. (2014) (Supplementary Information) that the spinup period was sufficient to get the upper ocean into equilibrium. A spinup period long enough to get the deep ocean into equilibrium was not envisaged due to the comparably high resolution used for this set of experiments. However, a spinup of 300 years was sufficient to get the vegetation coverage into equilibrium.

Model outputs shown in the following are annual or seasonal means, averaged over the last 100 model years. Differences in the Sect. 4 are defined as anomalies of the experiment with lowered topography with respect to the control simulation (HT minus CTRL and AF minus CTRL respectively).

4 Results

4.1 Vegetation response

Our model simulations reveal distinct changes in vegetation coverage for Africa due to the imposed alteration of topography. Figure 2 summarizes the percentage grass and tree-type vegetation coverage for the control simulation and the response (change in percentage areal coverage) to a lowering of East and Southern African topography and to a lowering of Himalaya and Tibetan Plateau. Tree-type PFTs in tropical Africa are basically broadleaf evergreen and broadleaf deciduous tropical trees. Grasses are mainly warm C_4 grasses. Shrubs are no distinct PFT but are included in the category of grasses. The experiment lowering African topography to 50 % of present-day level shows less grass and shrub coverage in the Savannah zones of Southern Africa than with present-day topography. This indicates dryer conditions with lower mountains. In the coastal zone of Southeastern Africa forest coverage vanishes completely. In the CTRL simulation the dominant forest PFTs here are broadleaf evergreen and deciduous temperate trees and are only found in the Southeastern coastal zone of South Africa. Tropical East Africa shows a denser grass and shrub coverage with the absence of elevated African mountains. Over West Africa hardly any change is detectable. In Central Africa grassland is the main type of vegetation coverage with lower African topography. Tropical rainforests in Central Africa are only found in the control simulation, when African topography is at present-day level. Lowering Himalaya and Tibetan Plateau leads only to a slight deficit in grasses and shrubs, and slightly larger tree coverage in the Central African region. West Africa is the only region that shows an unaltered rainforest coverage in case of changed topography be it African or Asian.

4.2 Precipitation response

As the characteristics of the vegetation cover depend strongly on the regional climatic conditions (especially on rainfall) we further evaluated the model results in terms of changes in long-term mean atmospheric conditions (annual and seasonal means).

With lower African topography, annual rainfall in Central Africa significantly decreases by over 800 mm (Fig. 3). This explains the lack of Central African rainforest without elevated mountains in Africa. Over East Africa precipitation is significantly higher in case of lowered African topography, which then leads to the observed larger percentage of grass and shrub coverage.

However, the effect of larger rainfall in all but boreal winter season (Fig. 4f, i, l) does not lead to the development of forests in East Africa. In general, low mountains lead to a precipitation distribution that is characterized by smaller amounts of annual precipitation in Central Africa and higher annual rainfall in the East. Furthermore, East African rainfall amounts during boreal winter (Fig. 4c) are hardly altered by the 50 % topography reduction. Hence the dry season is probably still too long to maintain tropical forest vegetation. The strongly reduced forest coverage of South-East Africa that can be observed with lower African topography is connected to a year-round persistent rainfall deficit. Just in a small coastal strip of Namibia and South Africa, rainfall is larger with lower African topography which might be associated with the decreased Benguela upwelling intensity and the warmer tropical Atlantic Ocean (Jung et al. 2014). The impact of African uplift on West African rainfall distribution is not strong enough to affect the regional biogeography.

Lowering the Himalayan and Tibetan topography leads to slightly increased rainfall over Central Africa, Southern Africa and the Sahel region. Over West Africa a rainfall change can be observed from the beginning of the rainy season to the height of the rainy season (JJA; Fig. 4h) and during the retreat of the ITCZ in boreal autumn (Fig. 4k) which is most likely connected to either a strengthening of the convective activity of the ITCZ or a shift in the ITCZ. Only Central-East Africa shows a decrease in rainfall as response to lowering Himalaya and Tibetan Plateau, especially during southern hemisphere summer and autumn (Fig. 4b, e).

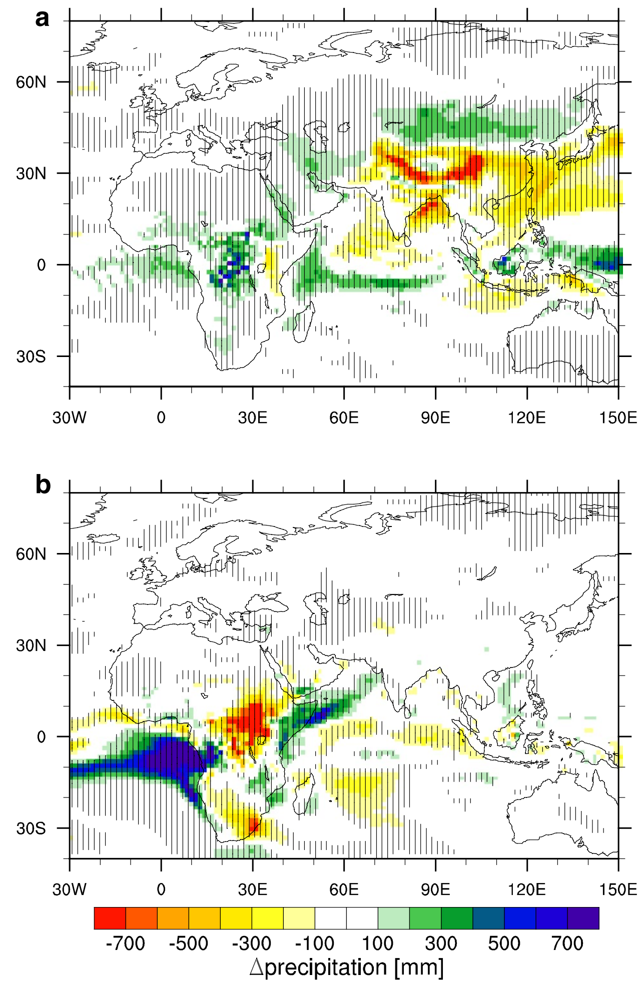

Fig. 3 Average annual precipitation responses (mm) to lowering of Himalaya/Tibetan Plateau (**a**) and of Africa (**b**), regions of high significance ($p < 0.01$) are hatched

4.3 Atmospheric dynamics

Most of the rainfall response signals can be explained by changes in moisture transport and convergence in the lower as well as in the middle troposphere. The former is connected to shifts and intensity changes of the ITCZ and changes in the strength of the low-level Somali Jet, illustrated at the 850 hPa level (Fig. 5); the latter is related to moisture transport through the AEJ, illustrated at the 650 hPa level (Fig. 6). Also related changes in atmospheric stability are displayed (Fig. 7). All major changes that are illustrated and discussed in the following are significant with a p value below 0.01 (t test).

4.3.1 *Impact of African topography*

Lowering African topography leads to a year-round prevailing reduced moisture transport to Central Africa. First there is

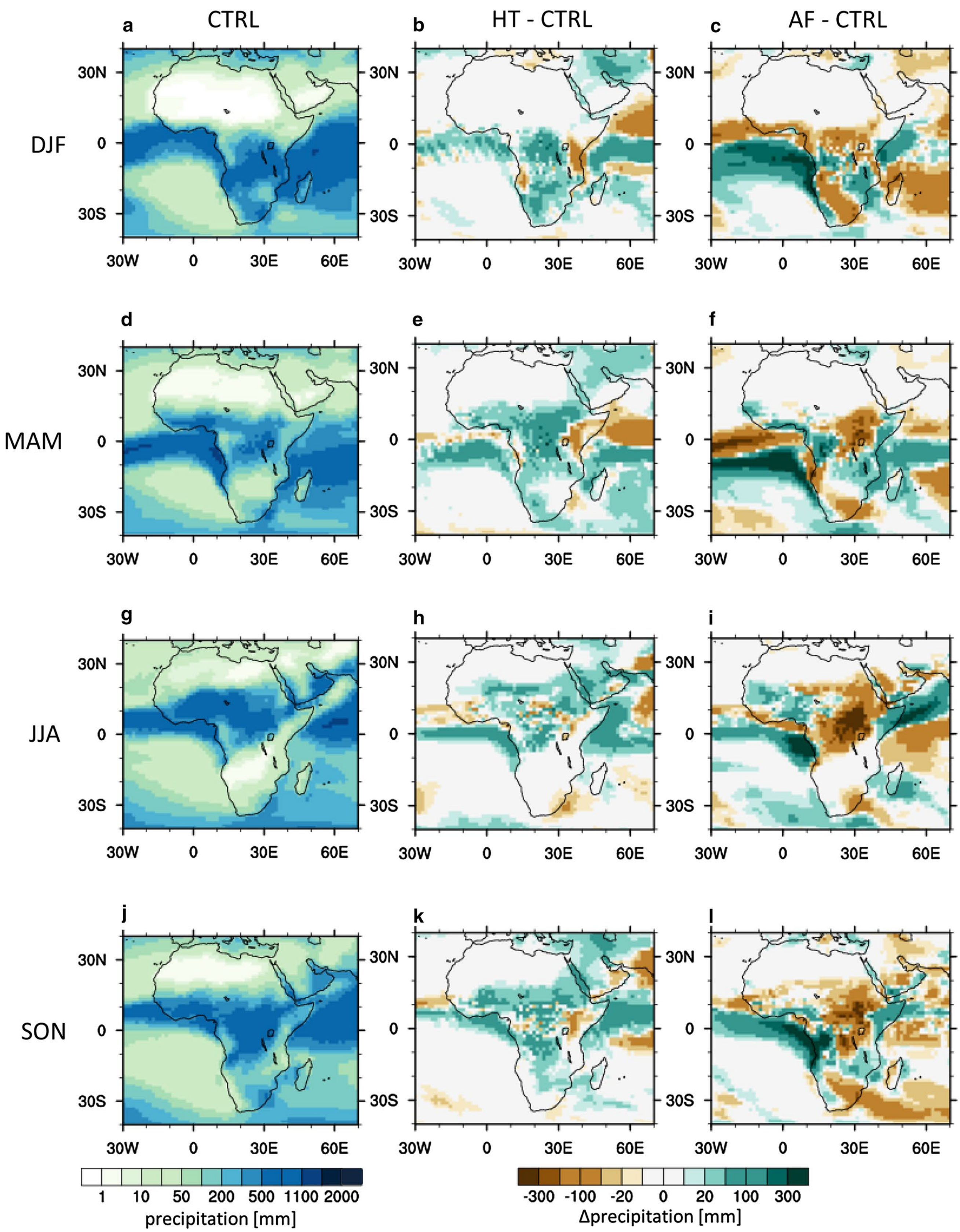

Fig. 4 Seasonal average precipitation (mm) for CTRL (**a**, **d**, **g**, **j**) and precipitation responses (mm) to lowering of Himalaya/Tibetan Plateau (**b**, **e**, **h**, **k**) and of Africa (**c**, **f**, **i**, **l**). Seasons: DJF (**a**, **b**, **c**), MAM (**d**, **e**, **f**), JJA (**g**, **h**, **i**), SON (**j**, **k**, **l**)

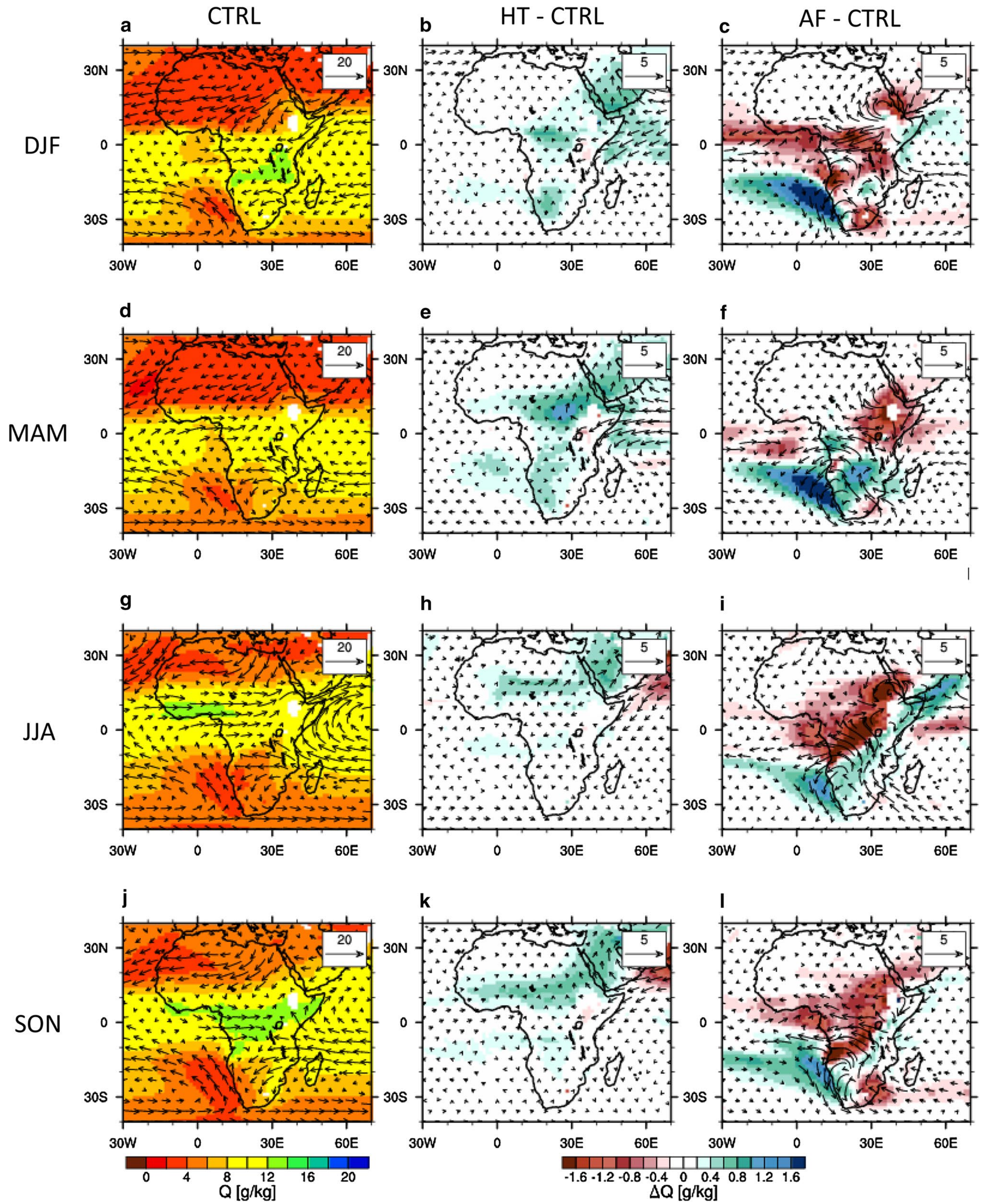

Fig. 5 Seasonal average specific humidity and horizontal wind (m/s) at 850 hPa for CTRL (**a**, **d**, **g**, **j**) and responses to lowering of Himalaya/Tibetan Plateau (**b**, **e**, **h**, **k**) and of Africa (**c**, **f**, **i**, **l**). Seasons: DJF (**a**, **b**, **c**), MAM (**d**, **e**, **f**), JJA (**g**, **h**, **i**), SON (**j**, **k**, **l**)

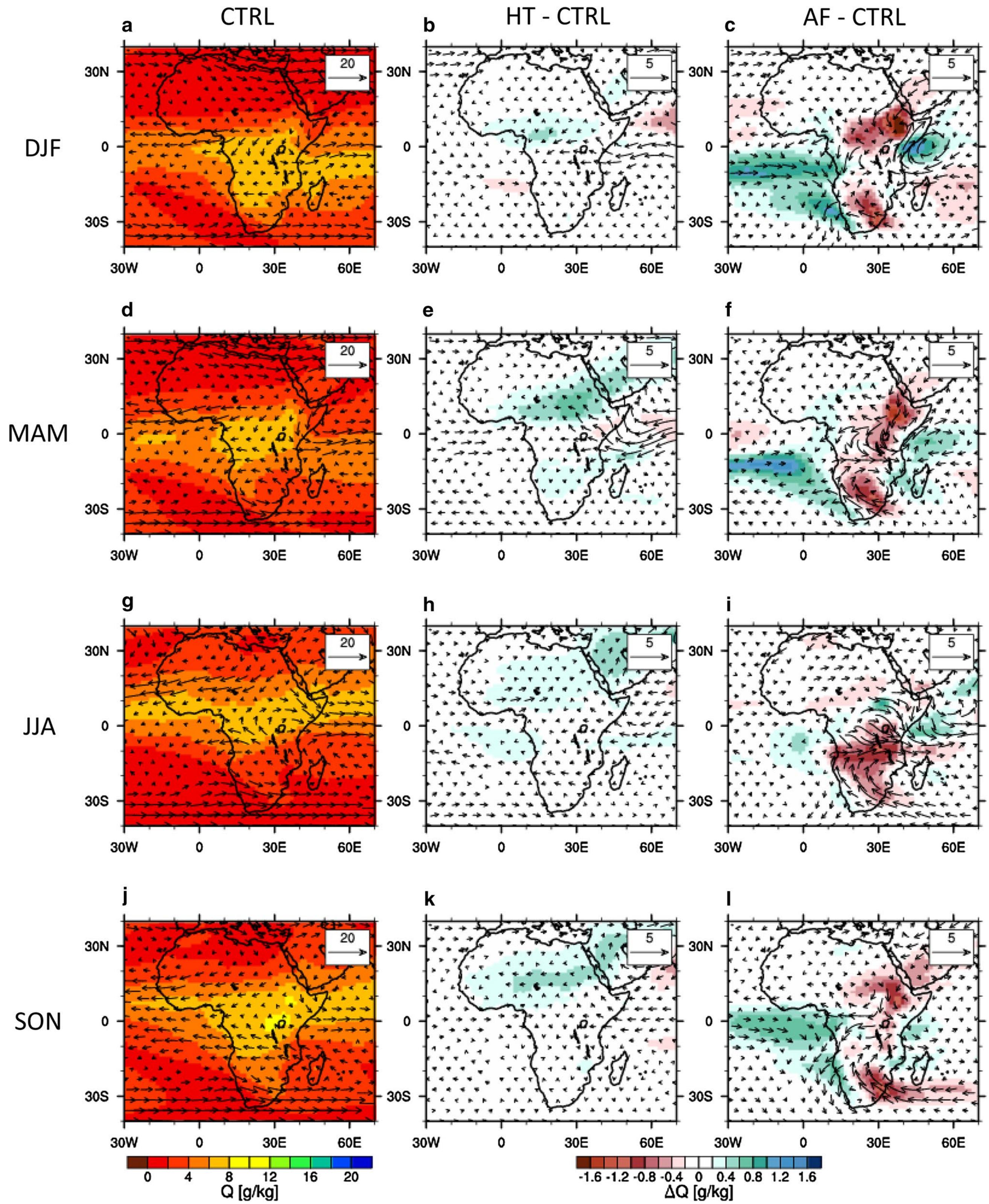

Fig. 6 Seasonal average specific humidity and horizontal wind (m/s) at 650 hPa for CTRL (**a**, **d**, **g**, **j**) and responses to lowering of Himalaya/Tibetan Plateau (**b**, **e**, **h**, **k**) and of Africa (**c**, **f**, **i**, **l**). Seasons DJF (**a**, **b**, **c**), MAM (**d**, **e**, **f**), JJA (**g**, **h**, **i**), SON (**j**, **k**, **l**)

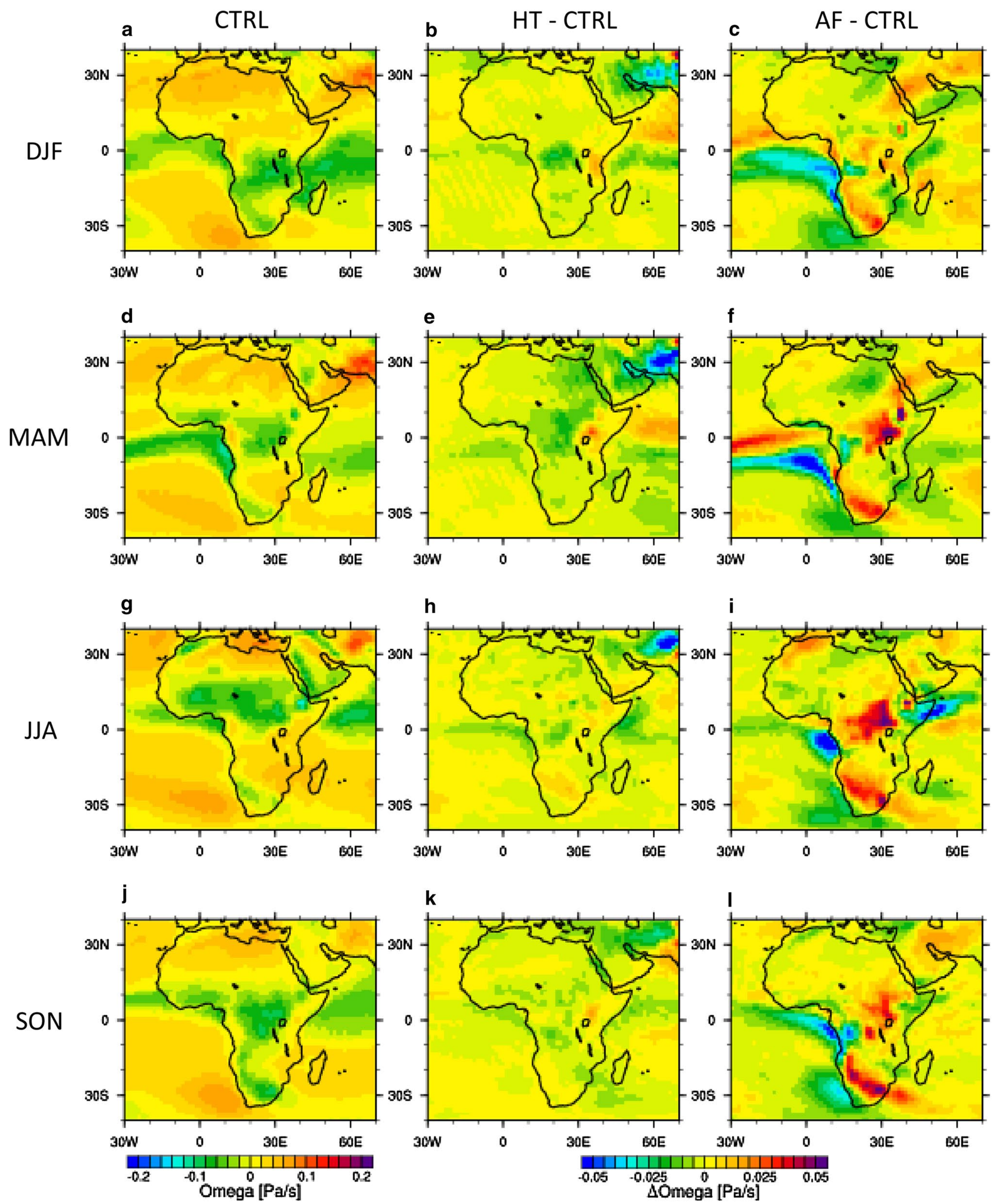

Fig. 7 Seasonal average vertical velocity component (Ω) at 500 hPa for CTRL (**a**, **d**, **g**, **j**) and responses to lowering of Himalaya/Tibetan Plateau (**b**, **e**, **h**, **k**) and of Africa (**c**, **f**, **i**, **l**). Seasons: DJF (**a**, **b**, **c**), MAM (**d**, **e**, **f**), JJA (**g**, **h**, **i**), SON (**j**, **k**, **l**) (positive Ω indicates downward motion)

a less intense moisture transport from the Atlantic to Central Africa (Fig. 5). The reason for this is most likely the weakening of orographically triggered convection with lower mountains, which leads to generally lower vertical velocities (compare Fig. 7), less deep convection and hence weaker moisture convergence at lower levels. A feedback between atmosphere and vegetation, which would lead to an enhanced drying and rainfall deficit (Akkermans et al. 2014) might also be at play. The summertime Somali Jet along the East African coast is weakened and less channelized (Fig. 5i) which leads to a decreased moisture transport away from East Africa to the Indian Ocean, causing wetter conditions over Eastern Africa in boreal summer. In boreal spring, mid-tropospheric inflow of dry air from northern directions is weakened over the Horn of Africa as illustrated at the 650 hPa level in Fig. 6f. This is probably causing a destabilization of the atmosphere and a reduction of subsidence (Fig. 7f), resulting in higher rainfall rates over the Horn of Africa.

4.3.2 Impact of Himalaya and Tibetan Plateau

One effect of the lowering of the Himalaya and the Tibetan Plateau is a weakening of the Somali Jet in boreal summer (Fig. 5h). But the jet weakening and the related effect of wetter conditions are limited to the Indian Ocean and are hardly found over Eastern Africa. Furthermore, in boreal summer a decrease of dry air input from the North, leads to the observed increase in precipitation in the Sahel region due to a destabilization of the atmosphere. At 650 hPa during the West African monsoon season, there is a weakening of the AEJ (Fig. 6h), which implies an additionally decreased moisture outflow from the African continent in the mid-troposphere due to lowering of Himalaya and Tibetan Plateau. For boreal spring (Fig. 5e) and winter seasons (Fig. 5b) the dry-air inflow at lower levels with the north-eastern trade winds to the Sahel and Central Africa is slightly reduced, which is most likely leading to a weakening of the stabilizing effect that the Harmattan has on the lower troposphere. Hence convection in Central Africa is enhanced. The decreased precipitation in East Africa in case of lowered Himalaya and Tibetan Plateau is also related to a reduced convective activity (compare vertical velocity component at 500 hPa; Fig. 7b, e, h, k).

5 Discussion

5.1 Comparison to other modelling studies

5.1.1 Atmospheric response to uplift

Our model results are qualitatively in agreement with other modelling studies considering African as well as global uplift regarding rainfall pattern change, even though the experiments differ strongly with respect to model type, setup, resolution, and magnitude of topography change applied.

According to a model study of Kitoh et al. (2010), global topography reduction does not show a strong effect on precipitation in Central Africa, but leads to a more uniform precipitation distribution in tropical Africa, with a closed rainbelt (in case of topography reduction to 20 % of present day), indicating higher rainfall rates at the Horn of Africa in boreal winter, as well as in summer. In their model simulations the distinct precipitation distribution we find today, with strongly reduced rainfall amounts over East Africa compared to Central Africa, is already apparent with 60 % topographic elevation of present day. In their coarse resolution (2.5° × 2°) study no striking change in Central Africa is simulated. Using a model of intermediate complexity, Schmittner et al. (2011) shows similar results when reducing topography completely, with wetter conditions over East Africa and only minor changes for Central Africa. For a systematic investigation of the effect of boundary condition changes a series of coarse-resolution (~2.8°) atmosphere GCM sensitivity experiments was performed with regard to the influence of land-sea distribution and orography in simulating first an Aqua planet world and then stepwise introducing land masses and topographic elevations of the continents (Xu et al. 2010a, b). It could be demonstrated that for the African region the presence of the land mass alone leads to enhanced precipitation over the Sahel/Sahara region and over Southern Africa. But the presence of African mountains turned out to be a prerequisite of pronounced rainfall to occur in Central Africa. This supports our results of strong rainfall increases in that area with African topography uplift. Himalaya and Tibetan Plateau uplift reduces rainfall in the Sahel/Sahara region, which is also in agreement with our model results. This effect is also discussed in Rodwell and Hoskins (1996) and Wu et al. (2009a).

In a study by Kaspar et al. (2010) a coarsely resolved atmosphere–ocean GCM (T30, ~3.75°) in a similar setup, lowering East and Southern African topography at different rates, an increase in rainfall is simulated over entire East and also some parts of Central Africa. A downscaling study using one of these global model outputs of a run with topography reduced to 50 % of the present-day level in a regional climate model (RCM) of ~50 km resolution was performed as well (Prömmel et al. 2013). This study demonstrates that the smaller precipitation response in Central Africa in the GCM is most likely caused by the low resolution of the model which limits the representation of the East African mountain ranges. In the RCM simulation clearly rainfall is decreased by the same order of magnitude as in our study over Central Africa. Also East Africa experiences stronger rainfall with lowered topography. The oceanic responses in the coarse resolution study by Kaspar et al. (2010) and in our study diverge largely, in that the warmer surface conditions of the Southern Atlantic under lower topography are not as strong (<1 °C, Prömmel, personal communication) as in our study (~2.5 °C; Jung et al. (2014)). Eliminating topography over East Africa completely in a coarse resolution (3.75° × 2.5°) atmosphere GCM (Slingo et al. 2005) shows a rainfall response over East (increase; but year round) and Central (decrease) Africa similar to that in Prömmel et al. (2013) and our study. In another atmosphere GCM simulation (Sepulchre et al. 2006) of higher resolution (~1° over the area of interest) a consensus with our study was found in wetter conditions in East Africa and dryer conditions over Central Africa, but also here topography was reduced to a much larger degree (5 % of present day level). This most probably leads to a reduced seasonality and stronger rainfall change over East Africa in DJF than in our simulation. However, the rainfall response to changed topography conditions in Central Africa is in a similar order of magnitude. Due to the finding that all these diverse model experiments with or without ocean model included yield similar results, it is unlikely that ocean–atmosphere feedback mechanisms are of major importance for the climatic response to altered topography.

5.1.2 Vegetation response to uplift

In the aforementioned study by Sepulchre et al. (2006) an atmosphere GCM was one-way coupled to a vegetation model. Even though there is some agreement in the rainfall response, there is a large discrepancy in the simulated vegetation coverage. No reduction of the Central African forest belt before uplift was simulated. Instead wetter conditions in East Africa without higher topography induced rainforest growth even there, leading to a closed forest belt over tropical Africa. Apart from the higher annual change in rainfall amounts this might be also due to the fact that in their simulation seasonality of rainfall in East Africa is reduced. This leads to increased water availability for plants year round. In contrast, in the study of Prömmel et al. (2013) an offline vegetation model driven by the output of their RCM simulation does not reproduce a closed forest cover over entire tropical Africa. Indeed, also with respect to vegetation, their simulation results resemble our model outcomes. The fact that similar rainfall changes in Central Africa lead to differences in vegetation response, especially regarding the distinctly different result by Sepulchre et al. (2006), suggests that the growing or non-growing of African rainforest most likely depends also on the land surface and vegetation models in use. Since none of the other models includes an interactively coupled dynamic vegetation module we further infer that vegetation–atmosphere feedbacks are probably of secondary importance, given the similar rainfall responses in the different models.

5.2 Paleo-climatologic context

For a comparison of the model results to proxy records of past vegetation and climate variables it would be necessary to place our sensitivity experiment results onto the paleoclimatic time line. This is not possible quantitatively due to the nature of the sensitivity studies that concentrate on the effects of isolated boundary condition changes. But also the timing of geologic and climatic processes and events is highly uncertain. One uncertainty is the temporal evolution of topography (Sect. 2.3), but also the temporal evolution and variability of rainforest coverage (Sect. 2.2) is not known precisely.

Nevertheless, we can find evidence that the processes relevant to our model results played a role in Earth's climatic history. We can demonstrate that under the given boundary conditions the mountains of Africa are an important prerequisite for Central African rainforest coverage to develop, and also that East African climate regime and vegetation are strongly altered by topography. Uplift processes were rather continuous and hence it is unlikely that these alone would lead to the observed highly variable climatic conditions and vegetation coverage (Kingston 2007). As Ruddiman et al. (1989) discussed, uplift might lead to an increase in the magnitude of orbitally triggered climatic variability. This effect of mountain uplift on African climate would fit well within the turnover-pulse theory of evolution of humans and carnivores in East Africa (Macho 2014; Vrba 1985) and also to the general tropical African vegetation evolution (Kingston 2007). Our results show that in East Africa the percentage area covered by grasses increases due to more favourable rainfall conditions with lower African topography. Proxy evidence indicates that a shift from C_3 dominated to C_4 dominated environmental conditions occurred in the late Miocene. According to Feakins et al. (2013) this shift was not necessarily connected to a shift towards much dryer conditions, but the region was characterized by a similarly open C_3 dominated vegetation before. Hence we suggest that our model simulations are qualitatively in agreement with the proxy records. Further on, the existence of Central African Miocene sand deposits (Senut et al. 2009) makes the simulated dryer conditions of Central Africa without elevated topography appear reasonable.

6 Summary and conclusions

According to our model simulations, precipitation is significantly lower in Central Africa and slightly higher in

East Africa in case of lowered African topography, leading to distinct differences in vegetation coverage. The effect of Himalaya and Tibetan Plateau elevation on African climate and vegetation is smaller, and generally shows the opposite direction (wetter conditions in Central Africa and dryer conditions in East Africa with lower topography). Additionally, lowering Himalaya and Tibetan Plateau leads to wetter conditions in the Sahel region. For tropical African climate the effect of African topography outweighs the effect of the Himalaya and the Tibetan Plateau. Lower African topography leads to an increase in vegetation coverage (mostly grasses and shrubs) at the Horn of Africa and the southern Arabian Peninsula. Nevertheless, according to our model results the rainfall increase over East Africa is not sufficient to maintain a densely covered rainforest.

The decreased rainfall amounts in Central Africa lead to a strong increase in grass coverage and a vanishing forest cover, when African topography is lowered to 50 % of present-day altitude. This indicates that, at least under current geographic boundary conditions, the elevated topography of Africa is crucial for the development of Central African rainforests.

A comparison with other model studies that varied largely in setup and complexity indicates that neither ocean–atmosphere, nor atmosphere–vegetation feedbacks seem to have a primary influence on the response signal to changes in topography. It would be valuable to test whether this holds true in a model intercomparison performed with a standardized model setup. Another conclusion that arises from the comparison of different studies is that the response in simulated vegetation to a similar change in rainfall does seem to depend largely on the used land surface/vegetation model. This highlights the necessity of further evaluation, intercomparison and improvements of land surface and dynamical vegetation models.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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