Vegetation development in West Africa of the biosphere shift during late Miocene to (early) Pliocene

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submitted by
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-Erklärung/Declaration-

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Bremen, den 26. September
The world is the geologist's great puzzle-box; he stands before it like the child to whom the separate pieces of his puzzle remain a mystery till he detects their relation and sees where they fit, and then his fragments grow at once into a connected picture beneath his hand.

Louis Agassiz
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Abstract

Aridification is a major aspect of the climatic trend in Africa during the late Neogene. Main causes of the aridification are changes in the atmospheric circulation as part of the steepening meridional pressure gradient. The trend is affecting biomes largely by shifting, shrinking and expanding vegetation belts. During the Miocene to Pliocene especially the tropical to subtropical savannah grasslands (C₄ grasslands) expanded. Triggers of the C₄ grassland expansion are not well understood and several mechanisms have been proposed explaining it such as decreasing CO₂ levels, aridification, increased seasonality and fire.

The thesis focuses on pollen, spores and microscopic charcoal records from a sediment core retrieved at Ocean Drilling Program Site 1081 offshore Namibia. The aim is to investigate the Miocene to Pliocene vegetation change of south-west Africa with emphasis on the expansion of the savannah grassland and the mechanisms behind it. Additionally, dinoflagellate cysts from the same sediments are analysed to study the link between continental and oceanic conditions.

In the first part (Chapter II) the focus is on the savannah grassland expansion. It was thought that decreasing CO₂ concentrations favoured globally the expansion of grasses during the Miocene/Pliocene. However, it was shown that the CO₂ concentrations of the Miocene to Pliocene were not changing significantly. Moreover, the expansion of grasslands occurred asynchronously on different continents enhancing the plausibility of regional to local drivers on each continent over one global trigger. The general competitiveness of grasses at higher temperatures and their adaptations to aridity and the occurrence of frequent fires support the hypothesis of aridification and fire as a driver of savannah expansion. The pollen and microscopic charcoal record in combination with carbon stable isotopes of plant waxes revealed that the savannah in south-west Africa expanded during an aridification period starting at around 8.3 Ma. Furthermore an extreme fire regime from 7.1 until 5.8 Ma favoured the C₄ grasses, which nowadays dominate tropical grasslands. As aridification continued shrubland and desert vegetation expanded and the grasslands became sparser during the Pliocene. In the remaining savannahs C₄ grasses increased and dominated the C₃ grasses.

In the second part (Chapter III) the general vegetation change in south-west Africa is studied. Using an unmixing model we show that the pollen and spore record revealed three steps of vegetation changes, which we interpret as the result of a continuous aridification process. A relative wet phase with higher representation of Cyperaceae, mountain and woodland vegetation is exchanged by a dry one with strongly increased abundances of desert and semi-desert...
indicators via a transition phase in which mainly grasses expanded. The results indicate ongoing aridification which is probably caused by the steepening meridional pressure gradient. In the last phase pollen from aquatic vegetation started to appear around 5 Ma, which we link to a relocation of the lower course of the Cunene River to its modern outlet in the Atlantic Ocean. Redirection of the Cunene River toward the Atlantic would have deprived the palaeolake Cunene of an important source of fresh-water ultimately resulting in the desiccation of the lake and the formation of the Etosha Pan.

The last part of the study (Chapter IV) focuses on the dinoflagellate cysts and the oceanic conditions along the Namibian coast. Changes in the assemblages of dinoflagellate cysts suggest a stepwise intensification of the Benguela Upwelling. During the late Miocene a higher influence of the southward flowing warmer Angola Current associated with a more southwards located Angola-Benguela front is likely caused by a weaker meridional pressure gradient. During the latest Miocene to earliest Pliocene the meridional pressure gradient steepened and the upwelling intensified. An intermediate period from 6.2 to 5.5 Ma is shown by the dominance of Habibacysta tectata, cysts of a cool-tolerant dinoflagellate known from the northern Atlantic, indicating non-reoccurring oceanic conditions, i.e. a change in the quality of the upwelled waters, which occurred during the Messinian salinity crisis. From 4.4 Ma on a stronger upwelling with well mixed nutrient waters is indicated.
Zusammenfassung


Der erste Abschnitt (Kapitel II) behandelt die Ausbreitung des Savannen-Graslandes. Es wurde angenommen, dass sinkende CO₂ Konzentrationen global die Ausbreitung der Graslandschaften während des Miozäns und Pliozäns antrieben. Jedoch stellte sich heraus, dass sich die Konzentrationen während dieser Zeit nicht ausschlaggebend veränderten. Zusätzlich breiteten sich die Savannen auf den Kontinenten nicht zeitgleich aus, so dass regionale bis locale Gründe für die Ausbreitungen wahrscheinlicher sind als globale. Wegen der guten Anpassung von Gräsern an hohe Temperaturen, Feuer und Trockenheit werden als Hypothesen zur Graslandausbreitung besonders die Austrocknung und Feuer als fundamentale Treiber genannt.

Die untersuchten Pollen und mikroskopischen Holzkohlenfragemente wurden mit einem stabilen Kohlenstoff Datensatz von Pflanzenwachsen aus denselben Sedimenten verglichen. Die Ergebnisse zeigen, dass die Savanne ab 8,3 Ma begann sich auszubreiten. Außerdem bevorzugte ein extremes Feuerklima zwischen 7,1 und 5,8 Ma speziell die Ausbreitung von C₄ Gräsern, die heute in tropisch bis subtropischen Graslandschaften dominieren. Unter anhaltender Intensivierung der Aridität breitete sich daraufhin Buschvegetation und Wüstenvestation aus, wohingegen die Graslandschaft sich ausdünnte. Hier zogen sich offensichtlich besonders C₃ Gräser zurück, so dass der relative Anteil von C₄ Gräsern in der Savannengraslandschaft zunahm.

Chapter I: Introduction

The climate of the earth changed in its history several times from a greenhouse to an icehouse climate and vice versa. The last 50 million years (Ma) were affected by general global cooling, from a greenhouse climate of the Eocene times to the Pleistocene glacial/interglacial climate (Zachos et al., 2001, 2008). The main driver during the cooling was the growth of ice shields on Antarctica and later on the northern Hemisphere. But besides that several further mechanisms are important for the cooling of the climate also influencing the growth of ice sheets, e.g. deep ocean circulation, global carbon cycling, changing oceanic currents and tectonic uplifts (e.g. Flower & Kennett, 1994; Zachos et al., 2001; Prange & Schulz, 2004). During the late Neogene, from 20 to 2 Ma, the East Antarctic Ice shield started to grow again after a warmer period, the mid-Miocene climatic optimum (Flower & Kennett, 1994). The growing ice sheets affected the climate by changing atmospheric circulations (e.g. Hadley cell circulation) and its intensities by increasing the meridional thermal gradients (Flower & Kennett, 1994). In general, wind systems, especially the trade winds become more intense affecting precipitation patterns towards aridification especially in the subtropics. Hence, this climate change had an intense impact on the biosphere shifting biomes (Pound et al., 2012). The aridification forced complete biomes to retreat or allowing them to expand and to evolve. During the mid-Miocene humid and warm conditions prevailed over subtropics and even in higher latitudes such as central Europe (e.g. Herold et al., 2011). From the late Miocene to Pliocene, deserts such as the Atacama Desert and the Namib Desert established (van Zinderen Bakker, 1975; Van Zinderen Bakker, 1984; Houston & Hartley, 2003). Furthermore, it is suggested that the general drier climate of the late Neogene favoured grasslands which expanded during the late Miocene to Pliocene especially in tropical and subtropical areas (Retallack, 2001; Edwards et al., 2010; Strömberg, 2011). Also in other parts of Africa the aridification took place and introduced the present biomes (Senut et al., 2009). Beside the Namib Desert and the Sahara Desert the aridification might have caused “the most dramatic example of biome assembly in the geological record”, the rise of C₄ grassland (Edwards et al., 2010).

1.1 Ecosystem savannah

Today grasses (Poaceae) inhabits all major landmasses and they dominate biomes covering in total up to 40 % of the earth’s surface (Strömberg, 2011) (Figure 1.1).
Considering Africa, the savannahs are the most dominant biome and inhabit tropical to subtropical areas. Within these biomes they form the natural habitat of specialized grazing and browsing animals, especially megaherbivores like Elephants, buffalos or giraffes (Uno et al., 2011).

Additionally, these herbivores serve as food source for predators which hide well in high grasses. The grassland savannahs especially of Africa are therefore a valuable ecosystem. Furthermore, grasslands are a unique environment closely linked to fires. Grasses are adapted to fires as a result of their fast re-growth after such disturbance. Fires control the tree cover and hence the boundary between grasslands and woodlands or forests by re-occurring annually or biannually (Bond et al., 2003; Bond, 2008; Furley et al., 2008). Therefore fires enable grasslands to prevail in areas were it is usually wet enough for trees. However, grasslands have also some feedbacks to the fire regime, e.g. by accumulating biomass which when dried provide as excellent fuel (Beerling & Osborne, 2006). This again creates a positive feedback leading to higher tree mortality.

1.2 $C_3$ and $C_4$ grasses

Principally, there are two different types of photosynthesis, $C_3$ and $C_4$. The $C_4$ pathway occurs in 18 different plant families including many subfamilies of the Poaceae. However, most $C_4$ plants are grasses (Sage et al., 1999a). In both physiological pathways the plants use the same enzyme (Rubisco) and the same biochemical cycle for carbon fixation (Calvin-Benson Cycle). However, the $C_4$ way has several carbon-acid products before whereof the first product has four carbons. As an anatomical feature in the leaves almost every $C_4$ plant has a kranz anatomy which acts as a CO$_2$ pump increasing the efficiency under lower atmospheric CO$_2$ conditions and/or higher temperatures (Ehleringer et al., 1997). This pump allows the plant under temperature stress to maintain energy winning while
doing photosynthesis and not switching to photorespiration as C₃ plants do (Tipple & Pagani, 2007). A further advantage is a higher water-use-efficiency as compared to C₃ plants under higher temperatures. C₄ grasses need only half as much water per unit carbon assimilation as C₃ grasses under 25°C (Hatch, 1987). In summary C₄ plants have advantages under higher temperature, aridity, high light conditions and lowered CO₂ concentrations (Sage et al., 1999b). As a by-product of the CO₂ accumulation within the C₄ photosynthesis the plant takes up a higher amount of heavier C isotopes, e.g. ¹³C as other grasses or even other plants like most trees and has therefore a special isotopic value (O'Leary, 1988).

1.3 Evolution of grasses and grasslands

The oldest known Poaceae fossils are phytoliths which are silica bodies on the leaves of many grasses. These silica bodies were found in sediments in India with an age around 66 Ma (latest Cretaceous) (Prasad et al., 2011). Based on these findings a phylogenetic analysis suggests an origin of the Poaceae between 129 and 107 Ma (Prasad et al., 2011). So that all lineages of Poaceae were already present before Gondwana broke apart explaining a today world-wide distribution of all sub-families (Prasad et al., 2005). The oldest isotopic evidence for C₄ photosynthesis in grasses was found in a special analysis of isolated grass pollen from the earliest Oligocene (Urban et al., 2010). True fossil evidence showing the typical C₄ kranz anatomy is described from Miocene sediments (Thomasson et al., 1986). However, the grasses expanded not before the late Miocene, and it seemed that they established between the late Miocene to Pliocene on all continents (Cerling et al., 1997; Jacobs et al., 1999). Decreasing atmospheric CO₂ concentrations were thought to have favoured the C₄ grasses and enabled the rise of the grasslands by crossing a CO₂-threshold (500 parts per million by volume (ppmv) at high growing-season temperatures) (Cerling et al., 1997). Reconstructions of palaeo-CO₂ levels, however, revealed that the threshold at 500 ppmv was already crossed in the Oligocene (Figure 1.2) and might be linked to the origin of C₄ photosynthesis in general (Pagani et al., 2005; Zachos et al., 2008). Furthermore, these reconstructions showed that the CO₂ level was from the Middle Miocene on always at comparable levels as before the industrial revolution. Instead of decreasing CO₂ concentrations the level even increased slightly at the end of the Miocene which would have been a disadvantage for plants using C₄ photosynthesis. Additionally, an increasing amount of studies about the rise of grasslands revealed that the expansions on the different continents and in different regions were not synchronous (Edwards et al., 2010; Strömberg, 2011). Hence, the direct driver for the expansion could not have been a global mechanism and the trigger must be sought on regional to local scales.


Introduction

Figure 1.2: Reconstruction of atmospheric CO₂ concentration since the Eocene (after Zachos et al., 2008) showing that the atmospheric CO₂ threshold (500 ppmv) was crossed at the end of the Oligocene, long before the Savannah grassland expansion of the late Miocene. Additionally, it shows a small increase of CO₂ concentrations at the end of the late Miocene.

1.4 Motivation and objectives

Since it became clear that the reasons for the savannah grassland expansions are not linked to CO₂ the drivers must be of a more regional to local origin. However, the general cooling and drying of the globe within the Neogene aridification suited the grasses. Aridity is thought to be the immediate driver for the rise of grasses including a development of well pronounced seasons (Jacobs et al., 1999; Osborne, 2008; Strömberg, 2011; Scheiter et al., 2012). An enhanced seasonality enables during wet summers the build-up of biomass (e.g. grasses) which can act as fuel for possible fires whereas the flammability of this fuel increases during dry winters (Daniau et al., 2013). This climate suits grasses, especially, because they tolerate a long drying phase and can re-grow quickly when rains return. Additionally, since the present day boundary between woodlands and grasslands is defined by fires in many parts of the globe, fire is also thought to be a substantial driver for the expansion of grasslands fitting in the general idea of an increased seasonality (Jacobs et al., 1999; Keeley & Rundel, 2005; Beerling & Osborne, 2006; Tipple & Pagani, 2007; Osborne, 2008; Edwards et al., 2010; Scheiter et al., 2012). However, data showing the link between savannah grassland expansion and fire were not reported so far. To test these hypotheses this study focuses on vegetation changes in south-west Africa based on palynological investigations. The savannah grassland expansion of south-west Africa has not been investigated in detail, so that the present work will close a gap of vegetation history of Africa. In detail, the thesis focuses on three hypotheses:

I. Aridification took place during the late Miocene to Pliocene in south-west Africa favouring the savannah grassland expansion

II. Furthermore, fire was involved in the grass expansion

III. Regional aridification is linked to the development of the Benguela Upwelling
1.5 Present-day conditions

1.5.1 Climate and vegetation of south-west Africa

In Africa the climate range is wide, from tropical rainforest in the heart of the continent to the deserts and arid vegetation of e.g. the Sahara Desert and the south western parts of the continent (Figure 1.3).

![Figure 1.3: Modern vegetation cover of Africa representing climatic zones. Green colours represent forests, red to orange colours represent woodlands and shrublands, grasslands are in yellow colours, purple are agricultural used areas and in white are deserts (Mayaux et al., 2004)](image)

The distribution of those climate zones are linked to atmospheric circulations and oceanic interactions. For south-west Africa the South Atlantic Anticyclone (high pressure zone) is the most prominent feature influencing the entire sub-continent. The high is located at 27°S 10°W during austral winters whereas it moves south to 32°S 5°W during austral summers (Petterson & Stramma, 1991) (Figure 1.4). During the year a tropical low, Inter Tropical Convergence Zone (ITCZ) moves north and south. Towards its southern boundary it forms the Congo-Air Boundary (CAB) (Figure 1.4 and 1.5). This boundary divides the sources of air masses. To the west and north of the CAB the air masses derive mostly from the Atlantic whereas the air masses to the east are mainly derived from the Indian Ocean because the strong trade winds hinder the Atlantic air masses to penetrate further east (Gasse et al., 2008). Similar patterns are represented in the source of precipitation (Gimeno et al., 2010) (for precipitation over southern Africa see Figure 1.5). East of the CAB the
source of precipitation is the Indian Ocean and to the north and west the source is the Atlantic. The strong south-east trade winds, however, have a drying effect, so that the coast receives little rain.

![Atmospheric circulations over Africa in austral winter and austral summer](image)

**Figure 1.4:** Atmospheric circulations over Africa in austral winter and austral summer (Nicholson, 1996; Gasse et al., 2008). Note position shifts of the Inter Tropical Convergence Zone (ITCZ), the Congo-Air boundary (CAB).

Closely linked to the amount of rainfall is the distribution of vegetation. Towards northern parts of southern Africa, e.g. Angola, the precipitation is with over 800 mm per year high allowing woodlands and forest to grow (White, 1983; Giess, 1998). In more southern parts the precipitation decreases from the east to the west. Eastern parts of south-west Africa receive 250 to 500 mm per year. These areas are parts of the Kalahari savannah, often also called Kalahari Desert. Here the grass cover can be relatively dense, especially after rain. Up to 40% of the area can be covered by a closed canopy (White, 1983). In wide areas of south-west Africa, e.g. Namibia the C₄ contribution of the grassland is between 90 and 100% (Sage et al., 1999b; Still & Powell, 2010). With westwards decreasing amounts of rain, the vegetation is getting sparser and more desert-like. In areas receiving between 100 and 250 mm per year the Karoo shrubland prevails (White, 1983). This vegetation is dominated by shrubs and bushy plants, e.g. Compositae (or Asteraceae), Fabaceae or Acanthaceae (White, 1983; Cowling et al., 1998; Giess, 1998). Along the coast the aridity is most intense forming the Namib Desert. In the Namib the annual precipitation is in most parts less than 100 mm per year and is often so low that germination is impossible for most plants (Southgate et al., 1996) so that in some parts of the Namib vegetation is completely absent (White, 1983).

### 1.5.2 Oceanic conditions of the south-east Atlantic

The South Atlantic Anticyclone is influencing the surface currents in the south-east Atlantic by directing the Benguela Current northwards along the south-west African coast (Figure 1.5). The Benguela Current is fed by the cold...
eastward flowing Antarctic Circumpolar current and the retroflection of the Agulhas Current from the Indian Ocean. At 28°S the Benguela current splits into two currents, the northwards flowing Benguela Coastal Current (BCC) and the continuation of the Benguela Current (BC) which follows the atmospheric circulation of the SAA and turns westward towards South America (Figure 1.5).

![Figure 1.5: Map of location of ODP site 1081A (grey dot) in the southeast Atlantic. The mean annual precipitation of southern Africa (Nicholson, 2000) with the austral summer (1020 mbar in red) and austral winter (1024 mbar in yellow) position of the South Atlantic Anticyclone (SAA) (Pettersson & Stramma, 1991) and the Congo-Air-Boundary (Leroux, 1983) with the average summer position in red and the average winter position in yellow. Major Ocean features are Antarctic Circumpolar Current (ACC), Agulhas Current (AgC), Benguela Coastal Current (BCC), Benguela Current (BC), Angola Current (AC), the Angola Benguela Front (ABF) (Pettersson & Stramma, 1991). Bathymetry is indicated by fine grey lines.]

The BCC is furthermore linked to the trade winds which via Ekman-transport induce the Benguela Upwelling by pushing the surface waters offshore so that subsurface waters wells up (Lutjeharms & Meeuwis, 1987). These waters are derived from the Antarctic Intermediate Water which is cold and nutrient-rich. When these waters reach the photic zone biomass production increases significantly. Generally, the Benguela Upwelling is divided into 8 upwelling zones with different intensities and season maxima (Lutjeharms & Meeuwis, 1987). From these cells the winds push the upwelled water up to 600 km offshore producing filaments that mix with the south Atlantic surface waters. These mixed waters have still higher nutrient contents and lower SSTs (Lutjeharms & Meeuwis, 1987; Lutjeharms & Stockton, 1987; Summerhayes et al., 1995).

At around 15°S the BCC meets the southward flowing warm and nutrient-poor Angola Current (Figure 1.5) at the so-called
Angola-Benguela Front (ABF). The contact zone is composed of several fronts arranged into two zones, a northern and a southern one (Kostianoy & Lutjeharms, 1999). Depending on the meridional pressure gradient determined by the strength and position of the SAA, the southern frontal zone moves north or south. When the atmospheric pressure gradient is steep the ABF becomes narrower and sharper. However, when the SAA is exceptional weak the ABF shifts further south and allows the warm Angola Current to penetrate southwards as far as 24°S (Meeuwis & Lutjeharms, 1990). In this case the precipitation on the continent increases (Hirst & Hastenrath, 1983; Nicholson & Entekhabi, 1987; Rouault, 2003) which happens on inter-annual timescales similar to the El Niño (Shannon et al., 1986).

1.6 Climate during the late Miocene to Pliocene

During the Miocene to Pliocene the climatic conditions were different. Glaciations were unipolar with expanded ice shields only on Antarctica which caused a northwards position of all climatic zones relative to today, especially on the northern hemisphere (Flohn, 1981) and a weak meridional atmospheric pressure gradient. The still existing tropical sea gateways involved a different ocean circulation. Especially the closing of the Central American Seaway influenced the deepwater circulation from the late Miocene onwards, e.g. by stepwise increasing the north Atlantic deepwater formation (Billups, 2002). This pre-setting together with slightly higher CO₂ levels than today (around 400 ppmv) (Bartoli et al., 2011) enabled a general warmer and wetter climate during the late Miocene compared to today (Knorr et al., 2011). Since only the southern pole had extended ice shields the meridional pressure/thermal gradient was flat so that the winds were weak, too (Flower & Kennett, 1994). However, during the late Miocene the ice sheets on east Antarctica expanded again increasing the meridional pressure gradients and intensifying the winds (Flower & Kennett, 1994). Especially the strengthened trade winds had an impact on the ocean by inducing e.g. the Benguela Upwelling during the late Miocene (Siesser, 1980; Rommerskirchen et al., 2011) which had further influenced the precipitation on the continent. The upwelling together with the final closing of the Central American Seaway changed the ocean circulation in the Pliocene and introduced the modern cross-equatorial heat transfer from the southern hemisphere to the northern (Prange & Schulz, 2004; Salzmann et al., 2011). Vegetation and biome models suggest that due to the general warmer and wetter climate of the Miocene many nowadays arid regions were then covered with shrublands or woodlands (Pound et al., 2011). In Africa the vegetation of the Miocene is also indicating wetter conditions, however, with the intensification of the meridional pressure gradient the aridification started in southwest Africa, e.g. the Namib desert (Van Zinderen Bakker, 1984; Segalen et al., 2002).
Chapter I

The desertification progressed later in other parts of Africa, e.g. the Sahara which is thought to be arid since 6-7 Ma and east Africa which also shows an arid phase between 7 and 6 Ma (Bonnefille, 2010). A Niger delta pollen record showed that grasslands begun to spread in West Africa in the late Miocene probably also caused by aridification (Morley & Richards, 1993).

1.7 Material and methods

The material for this study is sampled of a core retrieved at Ocean Drilling Program Site 1081A (19°37.1818'S 11°19.1598'E) (Figure 1.5) in 4794.1 m water depth (Berger et al., 1998). The site is located around 160 km offshore Namibia on the Walvis ridge. The sediment is composed of olive-gray clayely nannofossil ooze and olive-gray to black clays (Berger et al., 2002). The age model is based on biostratigraphy, magnetic reversals and magnetic susceptibility resulting in sedimentation rates between 2 and 5 cm/ka (Berger et al., 2002).

Sedimentation at the site, on the one hand, is influenced by filaments derived from the Benguela Upwelling leading to increased productivity of e.g. phytoplankton. The high productivity creates good conditions for fossilization of a diverse microfauna and flora (e.g. cysts of dinoflagellates). On the other hand the easterly winds transport dust, pollen and spores as well as microscopic plant fragments to the site which are buried in the sediments.

Palynomorphs (e.g. pollen, spores and dinoflagellate cysts) are made of organic compounds such as sporopollenin or dinosporin which are resistant in non-oxidating environments. Since the high productivity at the site reduces the oxygen content in the sediments, the preservation of microfossils, e.g. palynomorphs, is enhanced (Wefer et al., 1998).

1.7.1 Palynological preparation

For the study a standard palynological preparation was followed (e.g. Traverse, 2007). At first each sample is measured with the water displacement method to specify the amount of sediment (usually around 5 cm³) which can be used later to calculate flux rates or accumulation rates of pollen and dinocysts. Additionally, each sample received a known number of indicator spores (Lycopodium clavatum). For the actual chemical treatment the sample was treated with ~5 % HCl to dissolve calcareous material and treated with ~20 % HF to dissolve silicates. The residuals were not exposed to KOH to avoid dissolving of sensitive organic-walled dinoflagellate cysts.

After neutralisation the residuals were sieved under ultrasonic treatment using a 8 µm screen effectively holding back particles bigger than 10-15 µm. The sieved and cleaned residuals were stored in water. For further investigation some drops of the residual were placed with glycerol on a slide to allow examination with a light transmitting microscope using magnifications of 400x, 600x and 1000x. For each sample at least 300 pollen and spores and 300 dinoflagellates were counted. Besides the pollen and dinoflagellate cysts also the number of charred particles (e.g.
microscopic charcoal) was counted. In the same slides the numbers of indicator spores were counted to calculate the concentration of the palynomorphs per ml sediment. The accumulation or flux rates of palynomorphs was then calculated by multiplying the concentration with the sedimentation rate after Berger et al. (2002).

1.7.2 Terrestrial palynomorphs
Terrestrial derived palynomorphs can be transported via rivers or by wind to oceanic sites. Spores derive from ancient plants such as bryophytes and ferns whereas pollen comes from angiosperms (flowering plants) and gymnosperms. Pollen and spores are very diverse and allow determining their botanical origin at least to family level. Although each plant species produces different amounts of pollen grains they can be used to reconstruct vegetation changes and to distinguish the source of origin. In the south-east Atlantic the buried pollen and spores were in most parts transported by winds. Dupont & Wyputta (2003) showed that the sediments along the Walvis ridge contain pollen and spores transported via easterly winds from the adjacent desert, semi desert and savannah. Hence, the sediment core 1081A can be used to describe changes in the vegetation of the continent.

1.7.3 Marine palynomorphs
Every dinoflagellate has ecological boundaries in terms of temperature, salinity or nutrients. For recent dinoflagellates laboratory and in-situ measurements can reveal those boundaries which enables us to use their fossil counterparts to reconstruct (palaeo-)environmental conditions (Dale et al., 2002; Marret & Zonneveld, 2003; Holzwarth et al., 2007; Zonneveld et al., 2013). However, older sediments contain cysts of extinct species with unknown ecological boundaries. For these species palaeo-distributions are the only tool to narrow down the environmental range of species. For the Miocene many modern dinoflagellates were already present allowing comparisons with modern values.

1.8 Thesis outline
In the following chapters I present the core of the thesis which is formed by three manuscripts accepted by or prepared for submission to peer-reviewed journals.

Chapter II: The Role of Fire in Miocene to Pliocene C₄ Grassland and Ecosystem Evolution (in press at Nature Geoscience)
Sebastian Hoetzel, Lydie Dupont, Enno Schefuß, Florian Rommerskirchen, Gerold Wefer
This study shows that fire was an important trigger in the establishment of the modern-like C₄ grassland in the Kalahari. A combination of a pollen, spore and microscopic charcoal record and a comparison with a carbon isotopic data set revealed that C₄ grasses were favoured during times of intensified fire activity. Therefore this studies answers hypothesis I and II.

Chapter III: Miocene-Pliocene Vegetation change in south-western
Africa (ODP Site 1081, offshore Namibia) (ready for submission to Palaeogeography, Palaeoclimatology, Palaeoecology)
Sebastian Hoetzel, Lydie Dupont, Gerold Wefer

The third study focuses on the details of the vegetation change during the Miocene to Pliocene. An endmember unmixing model was used to describe the vegetation change which resulted in three different phases: A relatively wet one with high representations of Cyperaceae, a dry one with high more desert and semi-desert plants, and an intermediate phase when especially grasslands expanded. These three phases represent ongoing aridification. Additionally, the study describes a sudden occurrence of aquatic vegetation indicators at around 5 Ma which is linked to a change of the course of the Lower Cunene. This redirection of the river might have been the main cause of the desiccation of the palaeolake Cunene on land into the present-day Etosha pan. This manuscript focuses on hypothesis I.

Chapter IV: Miocene-Pliocene Stepwise Intensification of the Benguela Upwelling over the Walvis Ridge off Namibia (ready for submission)
Sebastian Hoetzel, Lydie Dupont, Fabienne Marret, Gerold Wefer

The second manuscript focuses on the development of the Benguela Upwelling by describing community changes of dinoflagellate cyst assemblages. The results show that during the late Miocene the Angola-Benguela front was located further southwards and that intensification of the meridional pressure gradient let the front migrate northwards. As a consequence the upwelling intensified. During the Messinian Salinity crisis the quality of the upwelled water changed and enabled unique dinoflagellate communities to bloom. During the Pliocene upwelling intensified again and influence of freshwater input is suggested. This manuscript focuses on hypothesis III.

1.9 References


Introduction


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Chapter II: The Role of Fire in Miocene to Pliocene C<sub>4</sub> Grassland and Ecosystem Evolution

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2.1 Abstract
Modern savannah grasslands, in which grasses using the C<sub>4</sub>-photosynthetic pathway dominate, became globally established through the late Miocene to Pliocene (between 8 and 3 million years ago) (Edwards et al., 2010). Although this tropical savannah vegetation covers up to 40 % of the land surface (Strömberg, 2011), the particular processes driving Mio-/Pliocene C<sub>4</sub> grass expansion are still obscure. Several mechanisms have been proposed including decreasing atmospheric CO<sub>2</sub> levels (Cerling et al., 1997), increased aridity, and enhanced rainfall seasonality (Sage, 2001; Edwards et al., 2010; Strömberg, 2011). Recent studies suggest, however, that the role of fire in transforming ecosystems is underestimated (Keeley & Rundel, 2005; Beerling & Osborne, 2006; Osborne, 2008; Edwards et al., 2010). Here we demonstrate that grasses have expanded since 8 million years ago (Ma) in conjunction with increased aridity and enhanced fire activity in south-western Africa. This finding is based on pollen and microscopic charcoal records that are complemented by stable-carbon-isotope analyses of plant waxes derived from marine sediments of ODP Site 1081 offshore Namibia. The increased occurrence of fire favoured C<sub>4</sub> grass expansion and led to the establishment of modern-like C<sub>4</sub> grasslands. During the Pliocene, C<sub>4</sub> plants expanded further due to continuing aridification leading to the establishment of desert and semi-desert conditions. Our results confirm that ecological disturbance by fire provided an essential feedback mechanism in the establishment of tropical C<sub>4</sub> grasslands.
Eighty percent of the modern warm-temperate to tropical savannah grassland’s annual primary biomass production is by plants using the C₄ photosynthetic pathway (Sage, 2001). This type of photosynthesis evolved multiple times in different grass lineages starting around 30 Ma (Pagani et al., 2005; Vicentini et al., 2008; Urban et al., 2010), but large-scale expansion of C₄ plants did not occur until the Late Miocene (c. 8 Ma) (Edwards et al., 2010; Strömberg, 2011) and was previously thought to be synchronous on all continents (Cerling et al., 1997). Initially, decreasing atmospheric \( \rho \text{CO}_2 \) levels during the Neogene were assumed to be the main driver because C₄ plants are favoured over C₃ plants under low atmospheric \( \rho \text{CO}_2 \) (Cerling et al., 1997; Ehleringer et al., 1997). Atmospheric CO₂ concentrations, however, had probably already dropped below the critical threshold as early as the Oligocene (Pagani et al., 2005), i.e., long before the C₄ plant expansion. Recent studies on the expansion of C₄ grasslands in various regions have revealed globally asynchronous expansions (Edwards et al., 2010; Strömberg, 2011), which were often preceded by an expansion of C₃ grasslands (Edwards et al., 2010), for example, in North America and China. Hence, other environmental factors, like changes in the amount and seasonality of precipitation and disturbance by fires, have been suggested as potential triggers for the C₄ grass expansion (Keeley & Rundel, 2005; Beerling & Osborne, 2006; Osborne, 2008; Edwards et al., 2010). The fire hypothesis has been recently strengthened by vegetation modelling (Scheiter et al., 2012) but data to validate the role of fire are still missing. To understand the origin of the southern African C₄ grass savannah we conducted a palynological and biogeochemical study of sediments of Ocean Drilling Program (ODP) Site 1081 (Fig. 2.1) located 160 km off the Namibian coast (Supplementary Information), at the latitude of the modern grassland-woodland transition. Along the coast, desert and semi-desert prevail (White, 1983) as a result of intense aridity induced by upwelling of cold waters along the coast driven by the strong south-easterly winds (Dupont et al., 2005). Consequently, pollen, plant particles, microscopic charcoal and plant waxes are transported to the site mainly by south-easterly winds (Dupont & Wyputta, 2003) from areas located farther inland, such as the Kalahari. The Kalahari dry savannah today is a dry summer rain area (precipitation of less than 500 mm; in Namibia usually between 150 and 250 mm per year (White, 1983)) and consists of grasslands comprising up to 90 % C₄ plants (Still & Powell, 2010). In the Kalahari burning occurs regularly at the end of the dry period when the vegetation is driest whereas the coastal desert does not provide enough fuel for fires (Fig. 2.1).
We focused on pollen types from grasses and semi-desert and desert plants found in ODP Site 1081 to trace the evolution of arid ecosystems. We also counted microscopic charred particles reflecting past fire activities (Supplementary Information). In addition, we measured the stable carbon isotopic compositions ($\delta^{13}C$) of long-chain $n$-alkanes derived from the protective wax coating of leaf-bearing terrestrial plants (Eglinton & Hamilton, 1967) to estimate the relative C$_4$ plant contribution. Due to their enhanced carbon fixation mechanism, C$_4$ plants produce wax lipids with heavier $\delta^{13}C$ values (Vogts et al., 2009). In general, the $\delta^{13}C$ values of the $n$-C$_{31}$ and $n$-C$_{33}$ alkanes ($\delta^{13}C$ $n$-C$_{31}$, $\delta^{13}C$ $n$-C$_{33}$) for C$_3$ plants from rainforest and savannah vegetation average around -36‰ VPDB while those for C$_4$ grasses are around -22‰ VPDB (Vogts et al., 2009). Today, the $n$-C$_{31}$ alkane is present in all major vegetation types of south-western Africa, whereas the $n$-C$_{33}$ alkane is predominantly derived from savannah herbs and C$_4$ grasses in particular (Vogts et al., 2009).
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Figure 2.2: Miocene-Pliocene records from ODP Site 1081. a, Grass pollen percentages considering the total pollen and spore sum. Shading indicates the 95% confidence interval. b, Stable carbon isotopes (δ¹³C) of plant wax (n-C31-alkanes in green, n-C33-alkanes in yellow) in per mil Pee Dee Belemnite (‰ VPDB) with two sigma error bars. c, ratio of charred particles over the sum of charred particles, spores and pollen. d, Pollen percentages of semi-desert / desert vegetation considering the sum of pollen and spores excluding Poaceae. Shading as in a. e, Sea surface temperatures (°C) calculated from the alkenone unsaturation index UK'37.
The record of the grass pollen (Fig. 2.2a) ranges between 30 and 45% from 9 until 8 Ma and steeply rises from ~30% at 8.4 Ma to ~70% at 6.8 Ma in the Late Miocene, indicating that grasses expanded to form extensive grasslands in the Kalahari between 8 and 7 Ma. The δ¹³C values of n-C₃₁ (Fig 2.2b) increase from less than -29‰ before 7.1 Ma to -27‰ at 6 Ma and reach -26‰ by 5 Ma indicating that the increase of C₄ plants in the vegetation took place over a longer period. For the δ¹³C of n-C₃₃, the trend is stronger starting at around -30‰ and reaching -26‰ already at 6 Ma representing a significant change in the composition of the vegetation to a greater proportion of C₄ grasses (see Supplementary Information). The stable isotope compositions of plant waxes before 7 Ma indicate that C₄ plants represented a minor share of the vegetation. After 6 Ma, C₄ plants became a dominant component of the vegetation and a composition similar to the modern situation was established, which corresponds to δ¹³C changes in fossil ratite eggshells from the Namib region (Ségalen et al., 2006). Also in East Africa, grasslands expanded before the spread of C₄ grasses (Feakins et al., 2013). The grassland expansion in south-western Africa is accompanied by higher ratios of charred particles from 7.1 to 5.8 Ma (Fig. 2.2c), reflecting enhanced fire activity likely caused by the expanded grasslands providing more combustible material. Additionally, a pronounced dry season was necessary to dry out the vegetation, making it more susceptible to fire (see Supplementary Information) (Osborne, 2008). This period of enhanced fire activity was followed by a drier period starting at 5.8 Ma indicated by a rise of desert and semi-desert vegetation (Fig 2.2d) and a drop in Poaceae pollen and charcoal. The lowered charcoal abundance is a result of an expansion of desert and semi-desert vegetation, which decreased the fuel supply. The grass vegetation expanded again briefly at 4.8 Ma, as indicated by grass-pollen values of up to 81.5% together with an increase in the charcoal ratio. Afterwards, the grass-pollen curve fluctuates strongly, but generally shows a decreasing trend and finally stabilises at 3.3 Ma at values of around 60%. This, together with the increasing desert and semi-desert representation, indicates expanded deserts and semi-deserts with reduced fire potential due to further increased aridity. The δ¹³C values, however, continued to increase and the relative abundance of Poaceae pollen decreased after 4.8 Ma, which we interpret to reflect a shift towards a greater proportion of C₄ grasses within the grass community.

The initial grassland expansion in south-western Africa and especially the expansion of the desert and semi-desert vegetation over the entire record correspond to the onset and intensification of the Benguela Upwelling (Rommerskirchen et al., 2011). Decreasing sea-surface temperatures offshore Namibia (Fig 2.2e) were driven by intensified upwelling caused by strengthened trade winds, leading to aridification of the coastal region (Dupont et al., 2005). A
Further impact on the regional climate had the expansion of the grasslands itself by reducing the regional rainfall due to lower evapotranspiration compared to more tree- and shrub-spotted landscapes (Beerling & Osborne, 2006). Furthermore, grasslands are less efficient in moisture recycling and hence the expansion of grasslands intensified the dry season. Thus, the expansion of grasslands created a positive feedback of increased aridification, promoting higher fire activity as long as there was enough fuel to burn (Beerling & Osborne, 2006).

Today, fires have a strong influence on the composition of modern African vegetation, e.g., by shaping the border between woodlands and savannahs (Furley et al., 2008). Through multiple positive feedbacks of droughts and fires, burning accelerates the loss of tree cover and promotes C4 grassland expansion (Beerling & Osborne, 2006), as grasses are morphologically well adapted to fires and rebound much faster than trees (Bond, 2008). Vegetation modelling suggests that the exclusion of fire in the Kalahari savannah would increase tree cover by up to 80 % (Bond et al., 2003). A further ecological impact of fire would have been of an evolutionary nature, affecting selection processes on the composition of the grasses, e.g. by favouring different grass lineages containing C4 grasses. The grass lineage of Aristidoideae, an almost exclusively C4 clade, is most diverse and its members most widely distributed in those areas of South Africa where a distinct dry season prevails and the rate of disturbance is high (Visser et al., 2012). Members of the tribe Andropogoneae (also C4) mostly occur in areas that are frequently burnt (Visser et al., 2012). Today, members of both clades are common elements in Namibian grass floras (Klaassen & Craven, 2003).

Our findings thus suggest that fires were selecting and favouring ecologically better adapted C4 grasses over C3 grasses, so that the high-C4 plant fraction in the vegetation could proliferate. Aridification favoured first the expansion of grasslands and later the coastal desert and semi-desert vegetation. The grass expansion created massive accumulations of fuel for fires. An intensified fire regime was established because of a generally drier climate, an enhanced dry season, and a higher fuel supply. We propose that after fire triggered the initial establishment of C4 plants, providing essential conditions for the dominance of C4 grasses, the continuing aridification led to a retreat of grasslands in which the C3 grasses disproportionately declined, leading to a relative increase in C4 plants. Driven by the enhancement of the Benguela Upwelling the vegetation changed to sparse grassland and desert vegetation, starving the fire of its fuel. The decrease of grasslands combined with the expansion of desert and semi-desert vegetation dramatically reduced the fire occurrence in the Pliocene. Aridification and the corresponding greater fire activity probably also affected the vegetation in other regions where savannahs expanded during the Miocene. A palynological record from the Niger deep-sea delta shows that grass pollen...
and microscopic charcoal concurrently increased 7 Ma ago (Morley & Richards, 1993), indicating that fire also played a pivotal role in the development of grass-dominated mesic savannahs in West Africa.

We thus infer that an intensified fire regime caused by aridification triggered the establishment of C_4 plants in African grasslands and created preconditions for the domination of C_4 grasses in savannah grasslands, which had an irreversible effect on the evolution of African ecosystems.

2.3 Methods summary

For palynological analyses the sediment was treated with 5 % HCl and 20 % HF and all particles smaller than 10 – 15 µm were removed by ultrasonic sieving. The residuals were mounted on a microscope slide and analysed at a magnification of 400. For each sample at least 300 pollen and spores were counted, and additionally all charred particles. The statistical error (95 % confidence intervals) was calculated after Maher (1971).

For organic-geochemical analyses, sediment samples were extracted by accelerated solvent extraction using dichloromethane/methanol (9:1, three times for 5 min., 70 bar, 100°C). The total lipid extracts were separated by Al_2O_3 column chromatography using hexane/dichloromethane (9:1) to elute an apolar fraction and dichloromethane/methanol (1:1) to elute a polar fraction. The polar fraction, containing alkenones for U^K_{37} analyses, was saponified using 0.5 M KOH in methanol and re-extracted with n-hexane after addition of distilled water. Polar compounds were converted to trimethylsilyl-ether derivatives before U^K_{37} analysis by gas chromatography with flame ionisation detection (GC-FID). SST estimates were calculated using the equation of Müller et al. (1998), and errors calculated using duplicate analyses. Apolar fractions were purified by elution over Ag-impregnated SiO_2-columns to remove unsaturated compounds. Compound-specific stable carbon isotope compositions were analysed on a ThermoFisher Trace GC Ultra coupled via a combustion reactor to a Finnigan MAT 252 mass-spectrometer. Isotope values were measured against calibrated CO_2 reference gas. δ^{13}C values are reported in ‰ VPDB. An externally calibrated n-alkane standard was measured every 6 runs. Averaged absolute deviations from known δ^{13}C values were consistently < 0.5 ‰ VPDB. All samples were run at least in duplicate with a reproducibility of < 0.5 ‰ VPDB. Precision and accuracy of the squalane internal standard were 0.5 and 0.0 ‰ VPDB, respectively.

2.4 References


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2.5 Acknowledgments

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2.6 Author Contributions

Palynological data analysis was carried out by S.H. and biogeochemical data by F.R.; Interpretation was carried out by S.H., L.D., E.S., F.R. and G.W. Correspondence and requests for material should be addressed to S.H.
2.7 Supplementary Information

2.7.1 Material
The sampled 452 m-long core was retrieved in a water depth of 794.1 m on the Walvis ridge (19°37.1818’S 11°19.1598’E) and is composed of olive-gray clayey nannofossil ooze and olive-gray to black clays (Berger et al., 2002). The age model is based on biostratigraphy, magnetic reversals and magnetic susceptibility (Berger et al., 2002). Due to a narrow shelf and steep slope the distance to the coast was not largely affected by sea level changes. Microscopic charred particles, pollen and spores as well as plant waxes were transported predominantly by winds. Today only one larger river exists in the vicinity. The Cunene River was very likely not flowing into the Atlantic until the Pliocene but feeding a huge lake, the Cunene lake (Hipondoka, 2005).

2.7.2 Charcoal and charred particles
Microscopic charcoal and charred particles are produced when plants are burnt. During fires microscopic particles can be elevated within a heat plume reaching altitudes up to 5 km (Palmer & Northcutt, 1975) and transported via wind over large areas (Verardo & Ruddiman, 1996). Numbers of charred particles can therefore be used to reconstruct past fire activities (Tinner & Hu, 2003). We considered opaque rectangular shaped organic particles bigger than 10 µm (< 50 µm), e.g. true charcoal (burnt wood) and other charred plant particles. We suggest a similar source area for the recorded charcoal as for the pollen and spores. Today fires occur in north and east Namibia especially during austral-spring (September to November) (Silva, 2003) [NASA Earth DATA]. We expressed charred particles as ratios of those over the sum of charred particles, spores and pollen. Because both the pollen and spores and the charred particles are wind-blown, effects of wind strength via sorting are minimised.

2.7.3 Interpretation of the pollen record
Although grasses occur in almost all vegetation types in SW Africa (White, 1983) the main source area of Poaceae (grass) pollen for sediments of ODP 1081 is the Kalahari savannah (Dupont & Wyputta, 2003). Changes in the palaeo-record of grass pollen, therefore, represent primarily changes in the expansion of the Kalahari savannah. Poaceae pollen percentages of the early part of the record are comparable to modern values (Figure 2.3) suggesting largely expanded grasslands during the latest Miocene. Prior to 8 Ma the record suggests a patchy open grassland possibly mixed with Cyperaceae and differing thus from the modern vegetation.
Almost all the investigated sediment samples are dominated by grass pollen which is related to the wind pollination mechanism of grasses producing large amounts of well dispersible pollen grains. Because Poaceae are over-represented in the pollen record percentages of other pollen groups are based on the total pollen and spore counts excluding Poaceae pollen.

Typical origins of pollen of the desert and semi-desert elements are vegetation types along the coast of Namibia (White, 1983; Giess, 1998). The coastal desert vegetation is represented by pollen of Amaranthaceae (including the subfamily Chenopodiaceae) (Figure 2.4d). In the group of semi-desert taxa pollen of Euphorbia, Acacia spp., Boleophitos, Monechma, Nyctaginaceae and Riccia are included (Giess, 1998). Pollen of the desert / semi-desert group is always present (except for two samples at 7.96 and 7.8 Ma) but percentages increase only in the younger parts of the record. At 6.3 Ma and 6.1 Ma values of up to 11 % are recorded. From 5.8 Ma onward the pollen record of this group is steadily increasing reaching 23 % (of total pollen without Poaceae pollen) at 3.1 Ma suggesting hyper-arid conditions along the coast, which is coherent with the interpretation that desert / semi-desert vegetation expanded at the expense of savannah grasses and shrubs in the Pliocene. The desert / semi-desert vegetation would have produced less fuel to feed fires. The rise of δ13C alkanes during the Pliocene indicating further expansion of C4 vegetation
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may be attributed to an expansion of drought-adapted C₄ species from the Amaranthaceae, which is indicated by an increase of Amaranthaceae pollen at 3.2 Ma (Figure 2.4d) corresponding with a δ¹³C maximum.

Another significant pollen group including *Petaldium, Ruellia, Acanthaceae* spp., *Piliostigma, Colophospermum mopane, Brachystegia* and *Lycopodium* represents the woodland. Pollen from woodlands is present in the entire profile but fluctuations are minor and usually in the range from 5 to 10 % (Figure 2.4a). We suggest that they mainly originated from north-east Namibia or Angola and indicate a constant background signal.

*Cyperaceae* (sedges) are mainly but not exclusively growing in wetter areas such as riversides and along lakes. The initial pollen percentages are relatively high and increasing until 8.3 Ma with maximum values of 29 % (twice as high as in subsurface sediments (Dupont & Wyputta, 2003)), decline to low values until 4.6 Ma, and rise again to the end of the record (Figure 2.4b). The high *Cyperaceae* pollen percentages of the early part are linked to wetter conditions. For the period after 4.6 Ma we suggest a different origin probably related to a change in the course of the Cunene River. Prior to 4.6 Ma the Cunene River flowed into the Cunene Lake but was re-routed to the Atlantic Ocean afterwards. Discharge of the Cunene River into the Atlantic ceased the water flow into the Cunene Lake causing the onset of its desiccation leading to the development of the Etosha Pan (Hipondoka, 2005). The additional pollen source area enclosed by the Cunene River is indicated by the occurrence of pollen of aquatic indicators such as *Nymphaeaceae* and *Typha* in the marine sediments, which are missing in the older parts of the record.

### 2.7.4 Indications for aridification

The percentages of *Asteraceae* pollen are increasing until 6 Ma (Figure 2.4c) which suggest increasingly dry conditions, because many *Asteraceae* shrubs and annual herbs are even better adapted to water stress than grasses. The charcoal record also indicates aridification because the charcoal particles are derived from fires which more frequently occur with enhanced aridity (see below for additional factors influencing biomass burning). Additionally, the transport of microscopic charcoal is favoured under dry conditions because winds can more easily pick up dry dust (including microscopic charcoal). Further indication of aridification during the first period until 6 Ma is the decrease of *Cyperaceae* pollen percentages during this interval.

Over the studied period desert and semi-desert pollen percentages are increasing (Figure 2.4), in particular during the Pliocene when *Asteraceae* pollen abundances decline, which we interpret as an expansion of deserts and semi-deserts caused by intensified aridification along the coast.
Chapter II

2.7.5 $\delta^{13}C$ of plant-wax alkanes in C$_3$ and C$_4$ plants

Relatively large ranges of $\delta^{13}C$ values of $n$-alkanes are detected in plants under different environmental conditions, in particular for C$_3$ plants during water stress (Diefendorf et al., 2010). During water stress the plants close their stomata or develop less stomata to increase the water use efficiency and hence use more $^{13}C$ so that the $\delta^{13}C$ will become less negative (Farquhar et al., 1989). As each plant species has its environmental boundaries (e.g. humidity) under which it can exists and reproduce, its $\delta^{13}C$ values can be influenced by water stress on the short term resulting in a certain range of $\delta^{13}C$. We argue that under lasting non-favourable conditions, however, the plants cannot survive, so that changes in $\delta^{13}C$ on longer time-scales will reflect changes in vegetation composition and water stress might play only a subordinate role in affecting $\delta^{13}C$ values.

In the current vegetation of south-western Africa, the $n$-C$_{31}$ alkane is present in all main vegetation types, whereas the $n$-C$_{33}$ is predominantly present in savannah plants occurring in dry climates and, in particular, C$_4$ grasses (Rommerskirchen et al., 2006; Vogts et al., 2009). The $\delta^{13}C$ values of $n$-C$_{31}$ and $n$-C$_{33}$ of C$_3$ plants range between -30 and -42 ‰ whereas the $\delta^{13}C$ values of C$_4$ grasses

Figure 1.4: Percentages of pollen of a woodland taxa, b Cyperaceae, c Asteraceae, and d Amaranthaceae. Percentage calculation is based on the total counts of pollen and spores excluding Poaceae pollen.
are between -26 and -18 ‰ (Rommerskirchen et al., 2006; Vogts et al., 2009). An expansion of C₄ grasses would therefore show a stronger increase in the δ¹³C of n-C₃₃ than for the n-C₃₅ which indeed is observed during the first period of enhanced fire occurrence (Figure 2.2). However, due to the large ranges in δ¹³C values of plants of both photosynthetic pathways absolute estimates of C₃/C₄ plant ratios are difficult to constrain and associated with large errors. Therefore, we refrain from making quantitative estimates.

2.7.6 Seasonality, aridity, grasses and fire
A pronounced climatic seasonality as well as massive fuel are requirements for an intense fire regime (Osborne, 2008). Wet austral summers lead to accumulation of fuel by providing favourable conditions for grass expansion. An increase of rainfall by 200 mm per year (during the growing season) has been inferred to double the grass production (Daniau et al., 2013). Long enough dry winters increase the vegetation’s flammability (Daniau et al., 2013). In contrast, during dry summers less biomass will accumulate and during short dry seasons the vegetation will not so easily ignite. Both conditions lead to a less intense fire regime. Hence, we suggest that fire promoting conditions existed in the period of enhanced charcoal abundance and expansion of C₄ grasses. During the Pliocene the desert and semi-desert expanded on the cost of grasslands which is most probably caused by a decrease in overall rainfall and potentially a shift to a less fire promoting climate. A close connection of fire and C₄ grasslands in sub-Saharan Africa has already been demonstrated for glacial of the past one million years (Bird & Cali, 1998).

2.7.7 References


Chapter III: Miocene-Pliocene Vegetation change in south-western Africa (ODP Site 1081, offshore Namibia)

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3.1 Abstract

Aridification is an important aspect of Late Neogene climate change in south-western Africa probably caused by modifications in the atmospheric circulation in relation to the initiation and intensification of the Benguela Upwelling System due to globally steepening of the meridional pressure gradient. Intensification of the meridional pressure gradients influenced the climate intensively which had then an impact on the vegetation. However, vegetation changes of south-western Africa from the Miocene to Pliocene have not yet been reported and only indirectly investigated. Here, we present a pollen record of marine core ODP 1081A retrieved 160 km offshore Namibia covering the time between 9 and 2.7 Ma. Using an endmember unmixing model we distinguished three vegetation phases: a relative wet phase showing higher representations of Cyperaceae, a dry one with a strong representation of desert and semi-desert plants, and a transition phase when especially grasses expanded. The three phases indicate ongoing aridification probably caused by intensified meridional pressure gradients and shifts of the Congo-Air Boundary. Additionally, aquatic vegetation indicators appear in our pollen record from around 5 Ma on, which we attribute to a relocation of the lower course of the Cunene River to its modern outlet in the Atlantic Ocean. Redirection of the Cunene River toward the Atlantic would have deprived the palaeolake Cunene of an important source of fresh-water ultimately resulting in desiccation of the lake and the formation of the Etosha Pan.
3.2 Introduction

The vegetation distribution in south-western Africa is linked to climate, in particular to rainfall, which depends on the atmospheric circulation. Major features of the atmospheric circulation in south-western Africa are the Congo-Air boundary (CAB) (Fig. 3.1) and the strong south-east trade winds blowing along the coast (Nicholson, 2000; Gasse et al., 2008) that are responsible for the very dry environment of the Namib Desert in combination with the cold sea surface temperatures of the Benguela Upwelling System (Petterson & Stramma, 1991). Initiation of upwelling, implying the increase of the trade winds, is dated in the late Miocene between 10 to 15 Ma (Siesser, 1980; Diester-Haass et al., 1990; Heinrich et al., 2011; Rommerskirchen et al., 2011). Increase of the trade winds is attributed to a steepening of the meridional pressure gradient in association with global cooling during the late Neogene, when the climate shifted from the warm and humid conditions of the mid-Miocene to drier and cooler ones of the Plio/Pleistocene. Driven by the growth of the ice sheets on East Antarctica (Wright et al., 1992; Zachos et al., 2001; Billups & Schrag, 2002), the southern polar front moved northwards strengthening the meridional pressure gradient and the pressure systems on the Southern Hemisphere (Flower & Kennett, 1994; Zachos et al., 2001). In detail, the South Atlantic Anticyclone got stronger and so did the trade winds along the Namibian coast hindering air masses to penetrate into the continent. The late Neogene aridification started in the Namib region from which it spread over the African continent (Senut et al., 2009). In spite of the importance of the region, changes of climate and vegetation in south-western Africa are poorly investigated. Van Zinderen Bakker (1984) describes one palynological sample of Late Miocene age which might have been originated from a dry, very open vegetation in Namibia coeval with palms growing in the Cape Region (Van Zinderen Bakker, 1984). Most reconstructions of south-western African climate are based on sedimentological data. They are usually limited to the development of the Namib desert where fossil dunes (aeolianites) including ratite egg shells and other macro and micro faunal fossils were dated between 16 and 17 Ma (Pickford et al., 1995; Senut et al., 1998, 2009). Fossil fauna sites in the Namibian Serrgebiet (SW Namibia) indicate a mid-Miocene vegetation of woodland or open forest in an area that is extremely arid today (Senut et al., 2009). Stable carbon ($\delta^{13}$C) and stable oxygen ($\delta^{18}$O) isotope compositions of fossil ratite eggshells showed that the vegetation in Namibia changed and a C$_4$ grassy vegetation established through the late Miocene to Pliocene underlining aridification (Segalen et al., 2006; Dupont et al., 2013). In the greater Cape Flora Region (southernmost Namibia and west South Africa) more summer-drought and dry-adapted vegetation types gradually replaced tropical species during the late Miocene (Dupont et al., 2011). Wetter conditions for the late Miocene compared to those of the Pliocene are also suggested by modelling studies (Francois et al., 2006).
So far, a detailed vegetation reconstruction of the Late Miocene during the aridification in south-western Africa is missing. Here, we reconstruct the Miocene to Pliocene vegetation of northern Namibia based on the pollen and spore content of marine sediments from Ocean Drilling Program Site 1081 Hole A, retrieved offshore Namibia. We discuss the vegetation change in south-western Africa during the late Neogene and link these to the global cooling and aridification.

3.3 Modern regional climate and south-western African vegetation

Modern south-western Africa is climatologically controlled by aridity which is reflected in the vegetation (Fig. 3.1). There are two major gradients of decreasing annual rainfall, one directed north to south and the other east to west (White, 1983; Gasse et al., 2008). Along the coast precipitation is lowest and seldom reaches 100 mm per year causing the aridity of the Namib Desert. The Namib is characterized by extremely sparse and contracted vegetation, which consists of isolated plants. In some areas vegetation is completely absent (White, 1983). Inland parts of south-western Africa receive between 250 and 500 mm rainfall per year. Here, wooded grassland of the Kalahari...
savanna occurs. Between the Kalahari and the Namib lies the Karoo shrubland (Nama Karoo) receiving precipitation between 100 and 250 mm. Typically, the landscape in the Nama Karoo is dotted with shrubs or small bushy trees of families such as Compositae (or Asteraceae), Fabaceae and Acanthaceae (White, 1983; Cowling et al., 1998). Most of the precipitation in south-western Africa falls in austral summer, whereas in the South African Cape Region including the succulent Karoo the rain falls mainly during austral winter (Tyson & Preston-Whyte, 2000). The winter rain area in Namibia is very rich in endemic species, many of them belonging to Aizoaceae, Geraniaceae, and other families (Cowling et al., 1998). In northern Namibia the Zambezian woodland grows in a climate with very pronounced seasonality and precipitation ranging from 500 to more than 1000 mm per year (White, 1983). The woodland is defined as an open stand of trees forming a canopy of at least 40%. Between these wooded areas the ground is covered by grasses, herbs or shrubs. The vegetation is linked to rainfall which itself is linked to the atmospheric circulation. In the north humidity derives mainly from the Atlantic, whereas further southwards in the summer rain areas of south-western Africa including the Kalahari savanna, air masses derived from the Indian Ocean transported by the Easterlies are the major source of precipitation (Gimeno et al., 2010). Along the coast the strong south easterly trade winds hinder air masses to penetrate over the continent (Gasse et al., 2008). Where Easterlies and Atlantic derived air masses meet the Congo-Air boundary (CAB) is formed which is considered a southern branch of the Inter Tropical Convergence Zone (ITCZ). During austral summers the CAB is located around 20-15°S whereas during the winter it is located at 9-6°S (Leroux, 1983). The position of the CAB is determined by the global thermal gradient and the strength and position of the Hadley cell (Nicholson, 2000). Therefore it is very likely that the position of the CAB changed in the geological past.

3.4 Methods and material

The material was sampled from cores retrieved at Ocean Drilling Program Site 1081 Hole A (19°37.1818'S 11°19.1598'E) (Fig. 3.1) in 794.1 m water depth. The site is located 160 km off the Namibian coast and is influenced by upwelling and easterly winds (Berger et al., 1998). The sediment is composed of olive-gray clayey nannofossil ooze and olive-gray to black clays (Berger et al., 2002). The age model is based on biostratigraphy, magnetic reversals and magnetic susceptibility resulting in sedimentation rates between 2 and 5 cm/ka (Berger et al., 2002).

Seventy-one samples were taken with ages between 9 and 2.7 Ma and prepared for palynological investigation. Volume was measured using water displacement. For decalcification diluted HCl (5%) was used and afterwards the material was stored in diluted HF (~20%) for two days to remove silicates. Before the mineral dissolving step, two tablets with a known number of Lycopodium spores were added to determine...
the pollen and spore concentration per ml. The residuals were sieved under ultrasonic treatment to remove particles smaller than 10-15 µm. The cleaned residuals were stored in water and mounted in glycerol for investigation under a light microscope using magnifications of 400x and 1000x. For each sample at least 300 pollen grains and spores were identified and counted. For pollen identification Scott (1982), Ybert (1979), Bonnefille and Riollet (1980), Maley (1970), the African Pollen Database http://apd.sedoo.fr and the reference collection of African pollen grains of the Department of Palynology and Climate Dynamics of the University of Göttingen was used.

For calculating the pollen grain flux rates the pollen and spore concentration per ml was multiplied by the sedimentation rates of Berger et al. (2002).

We carried out a multivariate analysis using an endmember model unmixing procedure (Weltje, 1997). We used a version of the unmixer algorithm programmed in MATLAB by Dave Heslop in 2008. The program is specifically designed to analyse percentage data.

3.5 Results

3.5.1 Pollen percentages and pollen flux rates

The identified pollen and spores were grouped into vegetation categories (Table 1). Based on the total number of pollen and spores the percentages were calculated and plotted in Figures 3.2-3.5. Additionally, pollen flux rates are plotted in Figure 3.2.

Figure 3.2: Overview of the ratio of endmembers, the relative abundances of vegetation groups in a cumulative diagram, and the pollen grain flux ratios (logarithmic scale) over the studied record.
Pollen flux rates are generally high but somewhat lower in the lower part of the record before 5.3 Ma ranging from 3419 to 19,615 grains per cm² per ka. After 5.3 Ma the pollen flux becomes higher with a minimum of 10,288 and a maximum of 62,587 grains per cm² per ka. 152 pollen and spore types have been identified, of which 73 types occurred in more than five samples (Table 1, at the end of this chapter). We grouped the pollen taxa into a) desert, b) shrubland, c) Compositae, d) Poaceae, e) aquatic vegetation, f) mountain vegetation, g) woodland vegetation and h) Cyperaceae (Table 1) based on Giess (1998), Scott (1982), and White (1983). Most abundant are pollen from the families of Poaceae, Cyperaceae and Compositae. The desert group includes Tribulus and species of the Amaranthaceae (inclusive Chenopodiaceae).

The pollen record is dominated by Poaceae pollen. However, the period before 8-7 Ma is characterized by lower relative values for Poaceae (less than 45 %) and relatively high representations of Cyperaceae (up to 20 %), woodlands (around 10 %), mountain vegetation (reaching 10 %) and desert vegetation (around 5 %).

Between 7.5 and 4.5 Ma the Poaceae pollen abundances are high up to 82.7 % fluctuating between 60 and over 80 %. Especially the representation of Cyperaceae, woodlands and mountain vegetation decrease or are very low. From 5.3 Ma on representatives of the aquatic vegetation are present. After 4.5 Ma woodland is again slightly better represented with pollen percentages between 4 and 8 % instead of less than 4 %. Contemporaneously, Cyperaceae pollen is reappearing again reaching 8 %. Additionally, percentages of the shrubland (maximum at 8 % at 3.3 Ma) and the desert indicators (Amaranthaceae) scoring in EM1 (maximum at 8 % at 3.1 Ma) are increasing. After 4 Ma the Poaceae pollen percentages fluctuate around 60 %.

### 3.5.2 Endmember results

We used a model with three principal components or endmembers (randomly ordered and named EM1, EM2 and EM3) explaining over 98 % of the variance ($r^2 = 0.983$). Calculation of endmembers was stopped at 1000 iterations resulting in a convexity at termination of -1.92. Only pollen and spore types occurring in at least five samples were considered. In Table 1, we listed pollen and spore types and coefficients of determination for each component ($r_c^2$).

Sixty-four pollen and spore types had significant scores ($r_c^2 > 0.055$) using a confidence level of 0.95.

Hence, the pollen record can be summarised into the three Endmembers (Fig. 3.2). Basically there is a shift of the dominant contribution from the EM2 (9-7.5 Ma) via EM3 (7.5-5.3 Ma) to EM1 (from 5.3 Ma on). The contribution of EM3 disappears after 3.5 Ma. Although the majority of pollen does not score on one endmember only, the three endmembers differ clearly in their mixtures of pollen and spore types, which can be interpreted in terms of vegetation (Table 1). In most cases the pollen types
Chapter III

classified in a vegetation group score on one endmember. EM1 is mainly dominated by Poaceae pollen. Additionally, most representatives of shrubland and aquatic vegetation score highest on EM1 (Figure 3.3).

**Figure 3.3:** Relative abundances of pollen groups of which the individual pollen types have high scores on Endmember 1. ‘Desert’ comprises pollen of Amaranthaceae and *Merremia*, ‘Shrubland’ pollen of *Blapharis*-type, *Justicia*-type, *Euphorbia*, *Acacia*, *Neuradaceae* and spores of *Riccia*, and ‘Aquatic’ pollen of *Nymphaea* and *Typha*. Upper panel shows the ratio of EM1 compared to the other EMs.

Furthermore, Amaranthaceae score on EM1 (Table 1 and Fig. 3.3). Complementing, the Compositae *Pentzia*, *Berkeleya* and *Artemisia*-types score also high on EM1. The total contribution of EM1 on the total ratio is relatively low prior to 8 Ma and its peaks increases to 0.4 until around 6 Ma (Fig. 3.3). From 6 Ma on, the contribution rises to 0.8 at around 4.6 Ma and fluctuates then between 0.7 and 1. Cyperaceae and most pollen types of the groups woodland, mountain vegetation, and desert vegetation score high on EM2. Additionally, the Compositae pollen types *Cotula*, *Dicoma*, *Gerbera*, *Vernonia* and undetermined liguliflorae types score high on this endmember. EM2 is more prominent in the early parts of the record with contributions of 0.6 to 1 around until 8 Ma. From 8 to 7 Ma the contribution of EM2 decreases at levels below 0.4 and reaches zero between 6.4 and 6.2 Ma. Afterwards the contribution stays below 0.3 and is again zero from 4.9 until 4.5 Ma. Most vegetation groups have one or a few pollen or spore types scoring on EM3. The only category almost exclusively scoring on EM3 is the group of spores. Additionally, *Dombeya* (Malvaceae) and other Malvaceae, *Proteaceae* spp., *Phyllanthus* (Euphorbiaceae), *Commiphora* (Bursaceae), the Compositae pollen type *Senecio* and undetermined tubuliflorae types, have high scores on EM3. Poaceae pollen scores
almost as high on EM3 as on EM1. Until 7.7 Ma and after 4.3 Ma the contribution of EM3 is usually below 0.2 except for two spikes reaching over 0.3 (at 9 and 8.7 Ma). Between 7.7 and 4.4 Ma the percentages of EM3 fluctuate and reach highest contributions (close to 1) between 6.4 and 6.1 Ma.

Figure 3.4: Relative abundances of pollen groups of which the individual pollen types have high scores on Endmember 2. ‘Woodlands’ comprise pollen of *Peltalidium*, *Ruellia*, other Acanthaceae, trichothosulcate-type, *Brachystegia*, *Colophospermum mopane*, *Detarium*, *Grewia*, ‘Mountain’ spores of *Phaeoceros*, *Lycopodium*, *Mohria*-type and pollen of *Stoebe*-type, *Ericaceae*, *Olea*, *Podocarpus*, *Passerina* and other *Thymelaeaceae*, ‘Compositae’ pollen of *Cotula*-type, *Dicoma*-type, *Gerbera*-type, *liguliflorae* type, *Vernonia*-type, and ‘Desert’ pollen of *Aizoaceae*, *Monsonia*, *Welwitschia*, *Tribulus*. Upper panel shows the ratio of EM2 compared to the other EMs.
Figure 3.5: Relative abundances of pollen groups of which the individual pollen types have high scores on Endmember 3. ‘Compositae’ comprise pollen Senecio-type and tubuliflorae type, ‘Spores’ comprise Osmunda-type, Selaginella-type, spore-type 2 bacculate, spore-type 3 leiotrilete, ‘Woodlands’ comprise pollen of Dombeya and Malvaceae spp., and ‘Shrubland savanna’ pollen of Commiphora, Phyllanthus and Proteaceae. Upper panel shows the ratio of EM3 compared to the other endmembers.

3.6 Discussion
3.6.1 Transport and source of pollen and spores and the desiccation of Lake Cunene

The transport of pollen and spores to ocean sites is either fluvial or aeolian. To ODP Site 1081 pollen is mainly carried by easterly winds. The aeolian pollen sources are along the coast and in the hinterland covering areas of the Namib Desert, Nama Karoo and the savanna (Dupont & Wyputta, 2003). Sedimentological studies showed that the south-east trade winds and seasonal winds from the north-eastern sector have been present since the late Miocene (Ségalen, 2004).

Geochemical studies have shown that the perennial Cunene River also influences the sedimentation on the Walvis ridge (Bremner & Willis, 1993). Shi et al. (1998) suggested significant fluvial input from the Cunene River at a site located further north based on the occurrence of pollen originating from the Angolan mountains. Thus, a minor part of our pollen transport is probably fluvial. However, it is suggested that the Cunene River did not reach the Ocean until the Pliocene but was feeding a palaeolake, called Lake Cunene (Hipondoka, 2005).

The modern Etosha pan (Fig. 3.1) is described as a relic of the palaeolake Lake Cunene (also called Lake Etosha) (Hipondoka, 2005). The pan is the
topographical centre of the Owambo Basin which has sediments deposited mainly by the Cubango and Cunene Rivers. Both rivers dominated the sedimentation in the basin since the early Neogene (Dill et al., 2012). A micropalaeontological study revealed that a freshwater lake, Lake Cunene, existed since 16 Ma (Dill et al., 2012) and a sedimentological-palaeontological study showed that the lake existed until late Miocene or early Pliocene and then started to desiccate (Miller et al., 2010). The desiccation is attributed to a redirection of the lower course of the Cunene River in addition to aridification of the region (Hipondoka, 2005). It is assumed that the river relocated and connected Lake Cunene with the Atlantic Ocean by the end of the Miocene or the beginning of the Pliocene. Our pollen record supports the idea that the Cunene River started to discharge into the Atlantic by the beginning of the Pliocene. An increase in the pollen flux ratio at 5.3 Ma is probably the result of additional fluvial discharge of pollen. Since 5.1 Ma pollen of Nymphaeaceae and Typha (Fig. 3.5) regularly appears in our record together with an increase in the representation of Cyperaceae (sedges) and woodland. We interpret the occurrence of pollen from aquatics like Nymphaeaceae and Typha as the effect of drainage of a freshwater body, e.g. a lake. The desiccation of the lake might also have led to higher representations of halophytes like some Amaranthaceae species. The presence of aquatic indicators in the pollen record of ODP Site 1081 marks the start of fresh-water discharge into the Atlantic by the Cunene River and the desiccation of Lake Cunene shortly before 5 Ma.

3.6.2 Vegetation development

The pollen assemblages over the entire record suggest open vegetation based on the high Poaceae pollen percentages and relatively low number of pollen from trees. However, prior to 7 Ma representations of woodland are higher indicating wetter conditions. Another important component during this period is afromontane vegetation including Pasierna and Ericaceae. The mountain vegetation might have been relative wide-spread in Angola until 8 Ma. Furthermore, Cyperaceae pollen, originating from sedges usually growing in swamplike environments, is very abundant in the period before 7 Ma and almost twice as common than today (Dupont & Wyputta, 2003). In our interpretation it reflects open vegetation including small ponds, or a landscape with small rivers. Paradoxically, the Tribulus record, an indicator of the Namib Desert (Fig. 3.4, main contributor in the desert vegetation group) is also very high during the period. Although Tribulus is a typical desert plant, it grows in areas with intermittently access to water such as river banks of ephemeral rivers and Tribulus may form flower carpets immediately after rainfall (Scott, 1982; White, 1983). The occurrence of this desert indicator corroborates a mid to late Miocene age of the Namib Desert (Senut et al., 2009).

Between 8 and 7 Ma the representation of savanna vegetation increased as indicated by the records of Poaceae, Commiphora,
Phyllanthus and Protea (Fig. 3.5). In terms of pollen percentages, the latter taxa are underrepresented, because their pollen is dispersed by animals rather than wind. The period from the latest Miocene to the early Pliocene spanned the major expansion of savanna grasslands in many parts of the world (Cerling et al., 1997; Tipple & Pagani, 2007; Strömberg, 2011). Here, in south-western Africa the savanna started to expand at around 8.3 Ma as indicated by a rise in Poaceae representation (Figs. 3.2, 3.3, 3.5).

The maximum values of Poaceae pollen of more than 80 % (at 6 and 4.9 Ma) even exceed maximum values recorded for the Holocene (Dupont et al., 2007) suggesting that during the Miocene savanna grasslands expanded further and occurred more widely than today. We propose that the climate in terms of precipitation and the length of the wet season favoured the expansion of grasses, but also promoted fires. This is indicated by the charcoal record of ODP Site 1081 (same material as used in this study) representing increased fire activity between 7.1 and 5.8 Ma (Hoetzelt et al. 2013 Nature Geoscience). It is possible that barring fire the amount of rainfall in the Miocene would have been sufficient to enable a denser growth of trees and shrubs. The fire regime might have favoured grasses and suppressed woody vegetation as indicated by vegetation models of the Kalahari in which the tree cover increased up to 80 % if fire is excluded (Bond et al., 2003). The expansion of grasslands and the shift to more savanna is consistent with increased δ13C values of fossil ratite eggshells indicating more C₄ plants in the vegetation (Ségalen et al., 2006).

Decreasing relative abundances of Poaceae pollen indicates that grasslands remained important but might have become less dense after 5 Ma. Between 4 and 3 Ma elements from desert vegetation (halophytic Amaranthaceae) and shrubland became more abundant suggesting increasingly drier conditions.

3.6.3 Steps in aridification

The vegetation indicates that relative humid conditions still prevailed during the Late Miocene, which is conform to global climate reconstructions and modelling (Pound et al., 2011, 2012). A reason for a warm climate might have been slightly higher CO₂ values (Bartoli et al., 2011; Pound et al., 2012). Wetter conditions could be explained by generally warmer sea surface temperatures of the Southern Ocean prior to the closing of the South American Sea-way, as models suggest (Prange & Schulz, 2004; Lunt et al., 2007). Furthermore, an expanded warm pool would be associated with flat meridional temperature gradients, a slower Hadley circulation, and permanent El-Niño-like conditions (Brierley et al., 2009 and references therein). Together the warmer oceans and the weaker upwelling fit into a scheme with weak meridional pressure gradients explaining the wet conditions in south-western Africa during the Miocene.

The coastal desert developed in close relation to the onset of upwelling in the adjacent ocean 10 to 15 Ma ago (van Zinderen Bakker, 1975; Siesser, 1980).
During the initiation of the upwelling the meridional thermal gradient was low so that pressure systems and winds were weaker than today. The Congo-Air boundary might have been less well developed or less strong allowing more humidity to penetrate into the continent from the Atlantic (Dupont et al., 2013), which would explain the relatively wet vegetation of the hinterland (indicated by higher values for Cyperaceae and EM2) in combination with a desert strip along the coast.

The endmember model indicates three phases of vegetation development represented by EM2, EM3, and EM1, respectively. Based on the scores of the pollen types on each of the endmembers we interpret the shift in vegetation as the result of aridification, beginning before 8 Ma and continuing after 5 Ma. The increasing aridity is manifested by the still wide-spread grasslands starting to get less dense together with an expansion of shrubland vegetation around 4 Ma. Further aridification is suggested by the expansion of halophytic desert plants around 3.3 Ma (Fig. 3.3).

The increasing aridity is probably caused by atmospheric strengthening of the pressure systems, e.g. steepening of the meridional thermal/pressure gradient. The drivers for the steepening are twofold. Firstly, the pressure zones and the ITCZ might have been pushed northwards (on the southern hemisphere) as a consequence of ice sheet expansions on Antarctica (Billups, 2002), similar to the northward movement during austral winters. Alternatively the ITCZ contracted, as a result of compression of atmospheric circulation due to decreasing global temperatures (Collins et al., 2010). Secondly, the Atlantic Meridional Overturning circulation intensified at the end of the Miocene (Poore et al., 2006; Butzin et al., 2011) which led to a cooling, especially of the Southern Hemisphere by a strong heat transport from the Southern to the Northern Hemisphere (Prange & Schulz, 2004). Both led to an intensification of the trade winds (including upwelling), a stronger CAB and a more restricted transport of humidity from the Atlantic. Intensification of upwelling and therefore of trade winds since 10 Ma has recently been demonstrated by a study of ODP Site 1085 (Rommerskirchen et al., 2011). With the strengthening of the trade winds and the decrease of coastal SSTs, the major source of precipitation shifted from the Atlantic to the Indian Ocean leading to less precipitation over south-western Africa (Dupont et al., 2013). The resulting aridification would have favoured first the expansion of savanna and later the increase of desert and shrubland vegetation.

3.7 Conclusions

Miocene to Pliocene samples from the ODP Site1081 have been investigated for their pollen and spore content to reconstruct vegetation changes. The pollen record shows a continuing aridification manifested in three different steps represented by three endmembers. The earlier and wetter period runs from the beginning of the record until ca. 8 Ma and is characterised by stronger representations of swamp, woodland and
mountain vegetation. The period might represent weakly developed meridional pressure gradients and, therefore, weak atmospheric conditions. During the following period (8 – 5 Ma) savanna grasslands expanded in Namibia indicating increasingly arid conditions. Probably the meridional thermal gradient got steeper and wind systems more intense. The record is complemented by the third period (5-2.7 Ma) representing further aridification. This aridification is indicated by some reduction in grassy vegetation cover joined by an expansion of shrubland and desert vegetation.

Apart from the vegetation development, the record indicates that a rerouting of the lower course of the Cunene River to the Atlantic Ocean draining the palaeolake Cunene took place shortly before 5 Ma by the sudden appearance of *Typha* and Nymphaeaceae pollen in combination with generally higher pollen flux ratios.

### 3.8 Acknowledgements

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### 3.9 References


Miocene-Pliocene Vegetation change


Table 1: Identified pollen and spore types sorted into vegetation biomes of southern Africa after (White, 1983; Giess, 1998) and their score to the endmember (in percent). Riccia is sorted into semi-desert and shrubland savanna (Volk, 1984). In bold are the high scores. $r^2$ is the coefficient of determination. Family names after www.ThePlantList.org.

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<th>Family</th>
<th>Pollen/Spore Type</th>
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<th>EM2</th>
<th>EM3</th>
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Miocene-Pliocene Vegetation change

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**Aquatic vegetation**

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**other spores**

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Chapter IV: Miocene-Pliocene Stepwise Intensification of the Benguela Upwelling over the Walvis Ridge off Namibia

Sebastian Hoetzel¹, Lydie Dupont¹, Fabienne Marret ²& Gerold Wefer¹

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4.1 Abstract

Upwelling is a significant part of the thermohaline circulation of the oceans controlling largely the transport of cold waters to the surface and therefore influence global climate. The Benguela Upwelling System (BUS) is one of the major upwelling areas in the world, however previous reconstructions of the BUS mainly focused on the onset and intensification in southern and central parts but changes of the northern part have been rarely investigated. We hereby present an organic-walled dinoflagellate cyst record of ODP Site 1081 from the Late Miocene to the Pliocene and use it to reconstruct and discuss the upwelling history on the Walvis Ridge with a special focus on the movement of the Angola-Benguela Front (ABF). We show that during the Late Miocene the Angola Current flowed over the Walvis Ridge more frequently than today because the ABF was probably further southward located as a result of a weaker meridional pressure gradient. A possible strengthening of the meridional pressure gradient during the latest Miocene to early Pliocene intensified the upwelling along the coast and the upwelling’s filaments over the Walvis Ridge. An intermediate period from 6.2 to 5.5 Ma is shown by the dominance of Habibacysta textata, cysts of a cool-tolerant dinoflagellate known from the northern Atlantic, indicating changing oceanic conditions contemporaneous with the Messinian salinity crisis. From 4.4 Ma on a stronger upwelling signal is recorded with well-mixed nutrient-rich waters. Our results show a stepwise intensification of the BUS over a long period and a northward migration of the ABF.
4.2 Introduction

Today the Benguela Upwelling System (BUS) is one of the major upwelling areas in the world. Along the south-western coast of Africa, cold and nutrient-rich waters well up and provide best opportunities for high primary production. The onset of this system is supposed to be in the early Late Miocene (~10-15 Ma) (Siesser, 1980; Diester-Haass et al., 1990; Heinrich et al., 2011; Rommerskirchen et al., 2011) during a phase of global cooling. This cooling is part of the transition of a warm and humid variable climate to cooler and drier conditions of the late Neogene driven by changes of the Antarctic ice sheets (Wright et al., 1992; Zachos et al., 2001; Billups & Schrag, 2002).

Following the mid Miocene climatic optimum, the re-establishment of major ice sheets in East Antarctica at around 10 Ma led to a steeper meridional temperature gradient which strengthened climatic zones and intensified pressure systems and ocean circulations (Flower & Kennett, 1994; Zachos et al., 2001). As a result, the South Atlantic Anticyclone (SAA) became stronger including also the trade winds which led to increased productivity especially at around 6.5 Ma (Diester-Haass et al., 2002). The further growth of the ice sheets led to a northward migration of the polar front causing also a shift of the BUS (Diester-Haass, 1988; Diester-Haass et al., 1990, 1992). However, many studies focused either in the southern and central parts of the Benguela upwelling or only on the ocean side of the Walvis Ridge (Siesser, 1980; Diester-Haass et al., 1992; Marlow et al., 2000; Udeze & Obohikuenobe, 2005; Heinrich et al., 2011; Rommerskirchen et al., 2011) and neglected the movement of the boundary to the north, the Angola-Benguela Front (ABF).

Here we present organic-walled dinoflagellate cyst data covering the late Miocene to Pliocene (9 Ma to 2.7 Ma). Our focus of investigation is the Walvis Ridge which divides the Cape Basin and the Benguela Current from the Angola Basin and the warm waters of the Angola Current. Studies on dinoflagellate cyst distribution in surface sediments along the West African coast (e.g. Dale et al., 2002; Marret & Zonneveld, 2003; Zonneveld et al., 2013) allow good estimations of relative changes of oceanic conditions, e.g. in terms of temperatures, salinities and nutrients. In this study we aim to describe the changes of the northern parts of the BUS during times of global cooling and discuss its forcing mechanisms and influences.

4.2.1 The Benguela Upwelling System

Over the South East Atlantic the semi-permanent high pressure system, the SAA, is the dominating atmospheric feature located at around 32°S 5°W (austral summer) and 27°S 10°W (austral winter) (Petterson & Stramma, 1991). The SAA is also affecting the Benguela Current (BC) which flows northwards along the south-western coast of Africa. The BC is derived from the eastward flowing cold Antarctic Circumpolar Current (ACC), which is linked to the polar front and taking up parts of the warm Agulhas
Current (AgC), which is flowing from the Indian Ocean around South Africa (Fig. 4.1). At around 28°S the BC is dividing into two separate currents. One is following the rotation of the SAA by turning west crossing the Atlantic. The second current is flowing further northwards along the south-western African coast forming the Benguela Coastal Current (BCC). Additionally, the BCC is linked to the south-easterly trade winds. The trade winds push the coastal surface waters via Ekman-transport off shore inducing the upwelling of cold and nutrient-rich subsurface waters (e.g. Lutjeharms & Meeuwis, 1987). The upwelled nutrients allow a vast production of phytoplankton in the photic zone. Eight upwelling cells have been identified, of which the one west of Lüderitz Bay is the strongest persisting all year long resulting in the coldest surface waters of the BUS (Lutjeharms & Meeuwis, 1987). Up to 600 km off shore cold upwelled waters from the coastal upwelling areas mix with surface waters and form nutrient-rich filaments (Lutjeharms & Meeuwis, 1987; Lutjeharms & Stockton, 1987; Summerhayes et al., 1995). Water of these filaments has clearly enhanced nutrient values, lower temperatures and increased primary production.

**Figure 4.1:** Map with location of studied ODP Site 1081 and discussed ODP Site 1085 within the South East Atlantic showing the mean annual temperatures in colours (Ocean Data View, U.S. NODC World Ocean Atlas 2009), oceanic features in black and grey (AC: Angola current, ABF: Angola-Benguela front, BC: Benguela current, BCC: Benguela Coastal current, ACC: Antarctic Circumpolar current, AgC: Agulhas current) and main atmospheric features in white dashed lines (SAA: South Atlantic Anticyclone, 1020 mbar; L(low): 1006 mbar). Mean atmospheric sea level pressure cells of January after (Petterson & Stramma, 1991).

### 4.2.2 The Angola-Benguela Front

The BCC meets the southward-flowing warm and nutrient-poor Angola Current just north of the Walvis Ridge. Together they form the ABF which lays today between 14°S and 16°S (Meeuwis & Lutjeharms, 1990), depending on the season. In detail, it is not a single front but
Stepwise Intensification of the Benguela Upwelling

A couple of fronts arranged in two frontal zones, a northern and a southern, whereas the latter one is the one with a higher influence on the overall ABF's characteristics (Kostianoy & Lutjeharms, 1999). Like the coastal upwelling, the position of the front depends on the SAA; when the meridional pressure gradient is high, the southern front of the ABF is located further north and the ABF is narrower and sharper (Kostianoy & Lutjeharms, 1999). Under weakened SAA conditions and resulting weakened winds, the ABF can be located further to the south (Richter et al., 2010) so that warm nutrient-poor water of the Angola current can penetrate further southward, up to 24°S along the Namibian coast (Meeuwis & Lutjeharms, 1990). As a result, the precipitation on the adjacent coast is enhanced (Hirst & Hastenrath, 1983; Nicholson & Entekhabi, 1987) and can be increased farther inland (Rouault, 2003). The phenomenon occurs on inter-annual timescales and is called Benguela Niño for its similarity to the El Niño Southern Oscillation (Shannon et al., 1986).

4.3 Material and methods

The sampled sediment core was retrieved at the Ocean Drilling Program Site 1081 (19^°37.1818'S 11^°19.1598'E) in 794.1 m water depth. The site is located on the Walvis Ridge 160 km off the Namibian coast and is today influenced by filaments of the BUS. The sediment is composed of olive-gray clayey nannofossil ooze and olive-gray to black clays (Berger et al., 2002b). Sedimentation rates were calculated between 2 and 5 cm/ka using an age model based on biostratigraphy, magnetic reversals and magnetic susceptibility (Berger et al., 2002b).

Seventy-one samples were taken with ages between 9 and 2.7 Ma and prepared for palynological investigation. The volume of each sample was estimated by water displacement. For decalication diluted cold HCl (~5%) was used and afterwards the material was treated with cold HF (~20%) for two days to remove silicates. Prior to the HCl-treatment Lycopodium tablets were added. The residuals were sieved under ultrasonic treatment removing particles smaller than 10-15 µm. The cleaned residuals were stored in water and mounted in glycerol for investigation under a light microscope using magnifications of 400x, 600x and 1000x. For each sample at least 300 dinoflagellate cysts were identified and counted.

Identification of dinoflagellates was done after de Verteuil & Norris, 1992; Marret & Zonneveld, 2003; De Schepper & Head, 2009; Schreck et al., 2012. Brigantedinium spp. includes all round, brown smooth dinoflagellate cysts. Because Batiacasphaera micropapillata has a strong morphological overlap with B. minuta and both occur in the samples we adopted the nomenclature of de Schepper & Head (2008) and Schreck et al. (2012) in treating both species as one complex.

Each species was sorted ecologically after its assumed metabolism mechanism (autotroph and heterotroph, Tab. 2, at the
end of this chapter) and a heterotroph/autotroph ratio (H/A) was calculated. Percentages were calculated on the total number of dinoflagellate cysts counted. For calculation of the 95% confidence intervals of the relative abundances the equation of (Maher, 1971) was used. Accumulation rates of dinoflagellate cysts were calculated by multiplying the sedimentation rates (Berger et al., 2002b) with the cyst concentrations per ml, which was calculated based on the known number of Lycopodium spores added in the form of tablets.

4.4 Results
A total of 36 species were identified whereof the Brigantedinium spp. group is the most dominant one. In Figures 3.2 and 3.3 the percentages and accumulation rates of the most abundant species are shown.

![Figure 3.2](image-url)
In general, both relative and absolute trends show similarity for each species. The record has been visually divided into 5 zones. One I runs from the start of the record at 9 Ma to 7.8 Ma. This zone is mainly characterized by cysts of the *Batiacasphaera micropapillata* complex with values mostly around 20% reaching a maximum of 50%. *Impagidinium paradoxum* is well represented (generally over 10%) especially in the beginning with a peak over 20%. *Lingulodinium machaerophorum* is present in all samples of Zone I, with two exceptions, reaches values up to 20% at around 8.5 Ma, and decreases afterwards to a minor representation in the assemblages. Cysts of *Nematosphaeropsis labyrinthus* reach up to maxima of 15%. *Impagidinium* sp. 2 (De Schepper & Head, 2009) cysts are also present and make up around 5% of the assemblage and have a maximum of 20% at around 8.3 Ma. *Selenopemphix quanta* is only marginally represented in Zone I. *Brigantedinium* spp. have generally low values (around 5%) that rise at the end of Zone I to around 15%. Almost completely lacking in this interval are *Operculodinium centrocarpum* cysts. Zone II (7.8 – 6.2 Ma) is marked by a decline of cysts abundance of the *B. micropapillata* complex to less than 10% (and
less than 5 % around 7 Ma). Additionally the absolute values are decreasing from around 3000 cysts per cm² per ka to less than 1000. Values for *Brigantedinium* spp. and *S. quanta* cysts are increased in this zone but show decreasing trends towards the end of the Zone II at 6.5 Ma. Also *H. tectata* decreases from around 20 % to marginal occurrence at 6.5 Ma. However, an increasing trend shows the representation of *B. hirsuta* from low values of less than 10 % to more than 30 %. As in Zone I *L. machaeorophorum* is mostly represented with less than 10 % but peaks at ~7.5 Ma with 63 % of the assemblage. Again *O. centrocarpum* is lacking.

The next part, Zones III and IV, starts at 6.2 Ma and ends at 4.4 Ma and is characterized by *H. tectata* cysts in Zone III until 5.8 Ma and *B. hirsuta* and *Brigantedinium* spp. in Zone IV. *H. tectata* dominates the samples in the first period and reaches values between 40 and 50 %. Additionally, the *S. quanta* curve increases again until 5 Ma. *Spiniferites* spp. and *B. hirsuta* values are also increasing between 6 and 5 Ma. *Brigantedinium* has low relative abundances until 5.2 but reaches 40 % later in Zone IV. Not represented is *L. machaeorophorum*. The *B. micropapillata* complex is better represented in the period from 5.2 until 4.2 Ma with maxima around 25 %. At around 4.8 Ma *Impagidinium* sp. 2 is well represented and peaks twice at values between 20 and 30 %.

The last Zone (V) is defined by the representation of *O. centrocarpum* which is rising from a few percent at the start of the interval to 62 % at around 7.5 Ma. Towards the end *Brigantedinium* spp. and *Spiniferites* spp. cysts are increasing on the costs of *O. centrocarpum*.

In Figure 4.4 the accumulation rates of summed dinoflagellate cysts are plotted against age. The accumulation of cysts range between 6,600 and 113,000 per cm² per ka showing two periods with maximum rates at 8-6.5 Ma and 5.4-3.5 Ma.

![Figure 4.4](image)

**Figure 4.4:** Accumulation rates of all dinoflagellate cysts. Zonation follows Fig. 4.2.
4.5 Discussion

4.5.1 Dinoflagellates as proxies for environmental conditions

Off the 2377 modern motile species listed worldwide (Gómez, 2012) only between 10 and 20 % of them produce during their lifecycle a cyst that preserved well in the sediments (Head, 1996). The organic-walled cysts found in recent sediments around the world show a distribution that is related to sea-surface gradients in temperature, salinity, nutrients and sea-ice cover (de Vernal et al., 1997; Zonneveld et al., 2001, 2013; Dale et al., 2002; Marret & Zonneveld, 2003; Holzwarth et al., 2007). Therefore, it has been possible to use them as a tool for reconstructing surface waters conditions, e.g. nutrients and temperature, enabling past upwelling intensity variations. The dissolution of sensitive species such as *Brigantedinium* can not entirely be dismissed here but the relative high abundance of this taxa overall in the record, as well as the high total concentration values (Fig. 4.4) suggest a minor effect. Therefore, we are confident to use the heterotrophic versus autotrophic ratio (H/A ratio, Fig. 4.5). The H/A ratio indicates upwelling (Lewis et al., 1990) based on the fact that the autotrophic dinoflagellates are in strong competition to diatoms whereas the heterotrophic feed on diatoms and hence, a high H/A ratio reflects higher production. In our record the ratio (Fig. 4.5) is in good concordance to the total dinoflagellate accumulation (Fig. 4.4). Our results indicate four different regimes (discussed below), a weak upwelling regime with a stronger influence of warm waters from the Angola Current (Zone I), an increase of upwelling linked to the intensification of the meridional pressure gradient (Zone II), a period with exceptional conditions during the Mediterranean Salinity Crisis affecting the Atlantic overturning circulation (Zone III and IV) and a further intensification of the upwelling together with the effect of the Cunene River discharge (Zone V).

4.5.2 The Angola-Benguela Front

ODP site 1081 is located close to the modern position of the ABF, which offers opportunities to record changes in its position since the Miocene. The composition of the dinoflagellate cyst assemblages shows affinity to upwelling conditions over the entire record through nutrient indicating cyst species such as *Brigantedinium* spp., *S. quanta*, *L. machaerophorum* which is in accordance to an onset of the BUS before 10 Ma (Siesser, 1980; Diester-Haass et al., 1990; Heinrich et al., 2011; Rommerskirchen et al., 2011). However, fluctuations in accumulation rates and relative abundances, such as the presence or absence of *L. machaerophorum* and *O. centrocarpum*, indicate significant variability in the upwelling during the studied period. Open oceanic species, *Impagidinium paradoxum* (Dale et al., 2002; Zonneveld et al., 2013) and probably *Impagidinium* sp. 2 are stronger represented in Zone I and II (9 - 6.2 Ma) indicating warmer and less nutrient-rich environments. In this zone the *B. micropapillata* complex is well represented. Unfortunately, the ecological
background of the *B. micropapillata* complex is uncertain. However, Zegarra & Helenes (2011) suggest this complex to be an indicator for warm nutrient-poor waters because it is often recorded together with other warm-water indicators. Hence, we consider *B. micropapillata* as an indicator of relative warm nutrient-poor conditions. These conditions during the early part of the record might be interpreted as weaker upwelling and stronger influence of warm waters from the AC compared to later periods.

Prior to 8 Ma, sub-Antarctic $\delta^{18}O$ values indicate slightly warmer temperatures and less intense glaciations in Antarctica (Billups, 2002). The polar front was, therefore, weaker and situated more southwards and so was the SAA. Additionally, glaciations in the Northern Hemisphere were not yet extensive so that the meteorological equator might have been located further north than today creating a weak meridional temperature and pressure gradient in the Southern Hemisphere (Flohn, 1981). A weak meridional temperature gradient would shift the ABF southwards and allow the AC to penetrate southwards over the Walvis Ridge which is suggested by the presence of *L. machaerophorum*.

Today *L. machaerophorum* is not present in the BUS but in the area of the AC (Holzwarth et al., 2007). Additionally *L. machaerophorum* is an indicator for stratified warm nutrient-rich waters, e.g., after upwelling relaxation (Marret & Zonneveld, 2003; Zonneveld et al., 2013; and references therein) suggesting that periods with stratified water conditions were more frequent and/or longer than today. In addition, today *I. paradoxum* and *N. labyrinthus* are more frequent in waters around the ABF (Dale et al., 2002; Zonneveld et al., 2013) and may indicate here a relation with the ABF. Today, the ABF shifts southwards on inter-annual timescales during Benguela Niño. Under these special conditions, the waters over the Walvis Ridge receive a contribution of the Angola Current (Petterson & Stramma, 1991; Florenchie et al., 2004; Mohrholz et al., 2004; Richter et al., 2010). It is possible that these Benguela Niño events were more common during Miocene times when the SAA and the trade winds were weaker. Richter et al. (2010) showed that sea-surface temperatures along the south-western African coast respond quickly to changes in the meridional wind anomalies. In detail, they showed that a weakening of the subtropical anticyclone led to warmer temperatures especially at 20°S.

### 4.5.3 Upwelling intensification and meridional pressure gradient

Zone II (7.8 – 6.2 Ma) shows higher overall dinoflagellate cyst accumulation rates indicating higher productivity as a result of stronger upwelling (Fig. 4.4). Further support of the intensified upwelling is given by increased heterotrophic dinoflagellate cyst occurrences, such as *Selenopemphix* and *Brigantedinium* (Zonneveld et al., 2001), which is also shown in the increased H/A ratio (Fig. 4.5).
Stepwise Intensification of the Benguela Upwelling

In general, a gradual intensification of the BUS is suggested by other authors, e.g. Rommerskirchen et al. (2011) who showed for ODP Site 1085 a continuously sea-surface cooling until 6 Ma. However, at the Walvis Ridge during this interval, periods of weaker upwelling and stronger influence of warmer waters may have occurred allowing the presence and even the dominance at 7.5 Ma of *L. machaerophorum*. Again, it is likely that the ABF was weaker and located further to the south and that the influence of the AC was stronger due to more frequently occurring Benguela Niño conditions. However, the influence of the AC seems to disappear towards the end of Zone II indicated by the decrease and low occurrences of *L. machaerophorum* and oceanic species such as *I. paradoxum* and the *B. micropapillata* complex. In contrast to the position of the ABF during the previous warm period, a northward shift and intensification of the ABF with the restriction of the AC as well as open ocean conditions can explain this change.

The growth of Antarctic ice sheets or the further global cooling (Billups, 2002) could have caused an increased meridional temperature and pressure gradient which resulted in stronger currents and winds. The strengthened winds, especially the trade winds, would lead to an aridification of the south-western coast of Africa since warm and humid air from the Atlantic would be hindered to reach large areas of Namibia, like it is today. The expansion of the grass savanna that took place between the Miocene and Pliocene, is often linked to aridification due to the water use efficiency of C₄ savanna grasses (Pagani et al., 2005; Ségalen et al., 2006). Additionally Dupont et al. (2013) discuss, based on pollen data and deuterium values of plant waxes from ODP Site 1085, that the aridification is caused by a decrease of precipitation derived from the Atlantic and that the main source area of precipitation changed to the Indian Ocean, which is the case today (Gimeno et al., 2010). Further support for the northward shift of the ABF is given by Diester-Haass et al. (1992) who argue that the BUS migrated northwards during the Miocene.

4.5.4 Exceptional conditions related to the Mediterranean Salinity Crisis

Zone III (6.2 - 5.5 Ma) is characterized by the dominance of *H. tectata* which is known
to be a cool-water tolerant species mostly of the Pliocene and Pleistocene of the North Atlantic region (Head, 1994; Versteegh, 1997; Louwye et al., 2004) but which is also recorded in the Miocene (Head et al., 1989) and the Mediterranean (Jimenez-Moreno et al., 2006). De Schepper et al. (2011) showed that if \textit{H. tectata} exceeded 30% of the dinoflagellate cyst assemblage, then the reconstructed Mg/Ca sea-surface temperatures were between 10 and 15 °C. Although \textit{H. tectata} has not yet been described from the Southern Atlantic, it probably represents strong surface water cooling and therefore intensified upwelling. According to Vidal et al. (2002), the sedimentation rate at ODP Site 1085 is increased during that period (6.1 – 5.8 Ma) which they correlate to the occurrences of strong glacial events. As a consequence, meridional pressure gradients steepened and upwelling further intensified. Additionally, \textit{S. quanta} is also increased during that period, indicating a higher nutrient supply supporting the interpretation of increased upwelling. Although the H/A ratio is lower than before it still suggests upwelling. Just before (end of Zone II, 6.8-6.4 Ma) and directly after the maximum of \textit{H. tectata} (Zone III-IV, 5.6-5.2 Ma), the occurrence of \textit{B. hirsuta} increased. However, the ecological background of \textit{B. hirsuta} is not well known. Both, \textit{H. tectata} and \textit{B. hirsuta} have not been yet described in the BUS area but they alternatively dominate the assemblages from 6.8 to 5.2 Ma, representing unique conditions which did not exist before or after that period. The representations of \textit{H. tectata} and \textit{B. hirsuta} fall in a period of global oceanic and climate changes and occur contemporaneously to the initiation of the North Atlantic Deepwater (NADW) formation, the desiccation of the Mediterranean Sea, and the loss of contact between the deep waters of the Pacific and Atlantic Oceans by the decreasing sill depth of the Central American Seaway (CAS). According to Billups (2002), the closure of the CAS had already influenced the ocean currents between 6.6 and 6 Ma by increasing the Atlantic overturning circulation. The data sets show a cooling of southern ocean upper circum-polar and intermediate waters during the latest Miocene. The influence of the closing of the Panama isthmus on the Atlantic overturning circulation is furthermore underlined by models such as the one used by Butzin et al. (2011) who conclude that the NADW formation began when CAS had shoaled to a few hundred meters during the Late Miocene. Poore et al. (2006) calculated the proportion of and describe a dramatic increase of NADW formation as well as a stronger Atlantic overturning circulation for the period between 6 and 2 Ma. Additionally, shortly before 6.2 Ma, the Mediterranean begun to desiccate, creating salty and dense waters flowing into the Atlantic and contributing to NADW formation (Pérez-Asensio et al., 2012). Hence, the overturning was further
increased and might have changed the overall oceanic conditions or at least might have had an impact on the upwelled waters of the BUS allowing the increased occurrence of *B. hirsuta*. Berger et al. (2002a) argued that the quality of the coastal upwelling waters is linked to the deep water circulation and the strength of the NADW. Increasing NADW brings, until a critical point, more silica from the Northern Ocean into the Southern Ocean (fire-hose effect) and so changes the chemistry of the upwelled waters at the BUS (e.g. enabling the so-called Matuyama Diatom Maximum). Changes of the silica content might have affected dinoflagellates indirectly via ecological competition with algae or other microorganisms or via changes in food supply and sources. The latter one is important for the heterotrophic species since they feed on diatoms which are highly depending on silica contents. Furthermore, Berger et al. (2002a) argued that the change of subsurface waters through time was caused by vertical mixing of the NADW around Antarctica preventing higher opal concentrations off South Africa and so explaining the low diatom concentrations in the BUS during the Pleistocene. The quality of upwelled waters is therefore variable and changes in correspondence to the NADW, for instance, by varying the silica content.

For the period from 6-5.5 Ma, Rommerskirchen et al. (2011) described Tex’86 temperature estimates from ODP Site 1085 indicating warming of subsurface waters. They concluded that the subsurface water warming resulted from a downward mixing of heat caused by the cessation of the Mediterranean outflow which weakened the Atlantic overturning circulation and reduced the NADW formation. This period of warm subsurface waters at Site 1085 coincides with the increased representations of *H. tectata* so that the downward mixing might have had also affected the quality of upwelled waters at the ODP Site 1081 creating special and non-recurring conditions.

A further change of the quality of the upwelled waters could be caused by a poleward undercurrent flowing south from the Angola dome along the African margin transporting silica-rich, phosphate-rich and oxygen depleted waters (Berger et al., 1998) and increasing the fertile thermocline. A strengthening of this undercurrent and a higher silica content of the waters representing a mixing of the intermediate water and this poleward undercurrent is indicated by a radiolarian peak from 5.8 Ma until 5.25 Ma at ODP site 1085 (Diester-Haass et al., 2002). The peak in radiolarian could also explain a missing peak in the H/A ratio since radiolarian might have competed with heterotrophic dinoflagellates.

Despite the warmer subsurface waters, further upwelling and cooling of the sea-surface in the southern BUS during that period is recorded by Rommerskirchen et al. (2011) at ODP Site 1085. After 5.5 Ma, the Gibraltar strait opened and again very salty and dense water re-intensified the NADW formation and the overturning.
The intensified overturning might have had an impact on the Hadley circulation and enforced trade winds so that the upwelling got stronger indicated by a sharp increase of *Brigantedinium* spp. at around 5.3 Ma which is in correspondence to increased sedimentation rates at ODP Site 1085 (Diester-Haass et al., 2002). Additionally, the circulation overturning could have been enhanced because of relatively high sea level (Haq et al., 1987). The representation of the open oceanic species *B. micropapillata* and *Impagidinium* sp. 2, however, suggest that the upwelling was intermittently less intense between 5.3 to 4.4 Ma. In between, the upwelling intensity must have been strong since the accumulation rates show the highest values of the record during that period (Fig. 4.4). Additionally, a strongly increased primary production is also indicated by the high H/A ratio (Fig. 4.5).

### 4.5.5 Upwelling intensification and river supply

The presence and dominance of *O. centrocarpum* in the last zone (from 4.4 Ma on) indicate nutrient-rich and well mixed waters representing conditions adjacent to strong upwelling and/or river outflow (Dale et al., 2002). Although *O. centrocarpum* is a cosmopolitan species, it occurs in the South East Atlantic in vicinity to the upwelling area (Dale et al., 2002; Marret & Zonneveld, 2003; Holzwarth et al., 2007; Zonneveld et al., 2013). It is, additionally, represented in turbulent and well mixed waters at the boundary of coastal and oceanic waters (Wall et al., 1977; Dale et al., 2002). *L. machaeorophorum* is, however, completely absent, indicating that the partly warm stratified conditions of the Miocene have been completely replaced by stronger upwelling, better mixing, and cooler conditions. The increase of *Brigantedinium* spp. abundance and the still high H/A ratios underline nutrient rich conditions of strong upwelling.

During that time (4.4 Ma), further closure of the CAS and the emergence of the Panama Isthmus proceeded and led to the intensification of the overturning circulation and of the deep waters (Haug & Tiedemann, 1998) changing the intermediate waters of the BUS. From 3.2 Ma on, after warming of the Northern Hemisphere, the intensification of the Northern Hemisphere glaciation and the introduction to a bi-polar icehouse started causing a southward-shift of the Inter-Tropical Convergence Zone (Billups et al., 1999). The southward shift caused an intensified meridional pressure gradient and therefore an intensification of the trade-winds as well as linked upwellings. The dinoflagellate cyst flux decreases while the H/A ratio increases indicating again a change of the quality of upwelled waters. That is in correspondence to a shift of diatom assemblages at further south located parts of the BUS during that time (Marlow et al., 2000). These changes can be linked to a stronger influence of Antarctic Intermediate Water. The increase of *Spiniferites* at the end of the record might be linked to more coastal conditions and river input (Dale et al.,
An increased river discharge could also explain relative high occurrences of *O. centrocarpum*. The desiccation and outflow of the Cunene lake through the Cunene river is supposed to have started in the early Pliocene (Hipondoka, 2005).

### 4.6 Summary and conclusions

A record of organic-walled dinoflagellate cysts was used to reconstruct upwelling conditions over the Walvis Ridge from the Late Miocene to the early Pliocene in respect to its northern boundary the ABF. Upwelling related conditions existed over the entire studied period. A weak pressure system and a further south located ABF resulted in more frequently occurring Benguela Niño-conditions, which were recorded for the time before 7.8 Ma. The meridional pressure gradient steepened afterwards, with a northward migration of the ABF. The Benguela Niño-conditions were especially manifested by the occurrence of *L. machaerophorum*, a species blooming in warm stratified nutrient-rich waters in particular after upwelling relaxation. The intensification of the upwelling is shown by decreases of warm water indicating taxa and increases of cold and nutrient-rich indicators. Production was high until around 7 Ma and the portion of heterotrophic species was enhanced. Between 6.8 and 5.2 Ma, *B. hirsuta* and *H. tectata* were abundant during a period with exceptional oceanic conditions related to the Messinian Salinity Crisis. *B. hirsuta* occurred during times with enhanced NADW production and stronger Atlantic overturning circulation whereas *H. tectata* occurred during a time of reduced NADW production due to desiccation of the Mediterranean Basin. The shoaling of the CAS and later the intensification of the Northern Hemisphere glaciations enhanced the NADW production, the Hadley circulation and the upwelling in the Benguela area producing well mixed conditions over the Walvis Ridge from 4.4 Ma on. Remote influence of fresh water after the start of Cunene River discharge into the South Atlantic is indicated by the first occurrence of *O. centrocarpum*.

### 4.7 Acknowledgements

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### 4.8 References


Marlow J.R., Lange C.B., Wefer G., & Rosell-Mele A. (2000) Upwelling intensification as part of the Pliocene-


Stepwise Intensification of the Benguela Upwelling


Table 2: Recognised species ordered after metabolism.

<table>
<thead>
<tr>
<th>Autotrophic species</th>
<th>species 2 (De Schepper &amp; Head, 2009)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>aculeatum</td>
</tr>
<tr>
<td>Impagidinium</td>
<td>paradoxum</td>
</tr>
<tr>
<td></td>
<td>sphaericum</td>
</tr>
<tr>
<td></td>
<td>patulum</td>
</tr>
<tr>
<td></td>
<td>strialatum</td>
</tr>
<tr>
<td>Operculodinium spp.</td>
<td>centrocarpum</td>
</tr>
<tr>
<td></td>
<td>israelianum</td>
</tr>
<tr>
<td></td>
<td>janduchenei</td>
</tr>
<tr>
<td>Phentapharsodinium dalei</td>
<td></td>
</tr>
<tr>
<td>Lingulodinium</td>
<td>machaerophorum</td>
</tr>
<tr>
<td>Spiniferites spp.</td>
<td>ramosus</td>
</tr>
<tr>
<td></td>
<td>mirabilis</td>
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<tr>
<td></td>
<td>cf mirabilis</td>
</tr>
<tr>
<td></td>
<td>membranaceus</td>
</tr>
<tr>
<td>Acomosphaera spp.</td>
<td></td>
</tr>
<tr>
<td>Nematosphaeropsis</td>
<td>labyrinthus</td>
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<tr>
<td>Batiacashaera</td>
<td>micropapillata</td>
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<tr>
<td></td>
<td>hirsuta</td>
</tr>
<tr>
<td>Tuberculodinium</td>
<td>vancampoae</td>
</tr>
<tr>
<td>Pyxidinopsis</td>
<td>reticulata</td>
</tr>
<tr>
<td>Habibacysta</td>
<td>tectata</td>
</tr>
<tr>
<td>Ataxodinium</td>
<td>zevenboomii</td>
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<tr>
<td></td>
<td>confusum</td>
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</tbody>
</table>
### Heterotrophic species

<table>
<thead>
<tr>
<th>Species</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brigantedinium spp.</td>
<td></td>
</tr>
<tr>
<td>Selenopemphix quanta neproides brevispinosa brevispinosa conspica armageddonensis</td>
<td></td>
</tr>
<tr>
<td>Trinovantedinium glorianum papulum fergnomatum applanatum</td>
<td></td>
</tr>
<tr>
<td>Lejeunecysta spp. oliva sabrina</td>
<td></td>
</tr>
<tr>
<td>Quinquecuspis concreta</td>
<td></td>
</tr>
<tr>
<td>Sumatradinium soucouyanatae</td>
<td></td>
</tr>
</tbody>
</table>

**Unknown, further species**

<table>
<thead>
<tr>
<th>Species</th>
<th>Description</th>
</tr>
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</table>

| Sumatradinium soucouyanatae | |


Chapter V: Synthesis and Outlook

The main aim of the thesis was to investigate the Miocene to Pliocene vegetation change of south-west Africa. Furthermore the thesis focused on the mechanisms causing the savannah grassland expansion. The stated hypotheses were addressed and answered:

5.1 Aridification favoured the savannah expansion

The first and the second manuscript (Chapter II and Chapter III) focused on the vegetation development of south-west Africa from the late Miocene to Pliocene (9 - 2.7 Ma). The pollen and spore content suggests a progressive aridification represented by vegetation change. At the beginning of record wet conditions prevailed indicated by Cyperaceae (sedges) pollen and a wider expansion of mountain and woodland vegetation. Wet vegetation types were successively replaced by drier ones. From 8.3 Ma on the grasses expanded and the wet indicators decreased. Since grasses are generally better adapted to drier conditions the savannah was able to expand. However, advanced aridification led the grassland to become sparser after 4 Ma, when shrubland and desert vegetation expanded. It seems that especially C₃ grasses retreated from the savannah because the overall Poaceae pollen percentages decrease while at the same time the stable carbon isotope composition of plant wax (δ¹³C_wax) indicates increased C₄ contributions.

The aridification is a trend recognizable on the entire African continent (Senut et al., 2009) fitting the global cooling trend during the Neogene. A steeper meridional pressure/thermal gradient could have been the driver for these changes by intensifying the atmospheric circulation (Flower & Kennett, 1994). As a consequence the trade winds strengthened and the CAB might have shifted with the result that intensified trade winds would have hindered humid air masses from the Atlantic to reach further inland into the continent, which led to drier conditions in Namibia. In South Africa the climate changed from a summer to a winter rain climate (Dupont et al., 2011) during the same period.

5.2 Fire and its role in the savannah expansion

The charcoal record shown in the first manuscript suggests that a regime of intensified fires took place from 7.1 – 5.8 Ma. Intensification of fires is most probably the result of the aridification in combination with enhanced seasonality. During the humid season grasses would grow and build up fuel which flammability would increase during the dry period. From 7.1 – 5.8 Ma the balance between wet and dry periods obviously was excellent for promoting fires,
Synthesis and Outlook

whereby a sufficient amount of rainfall was essential. Daniau et al. (2013) showed for the last 170,000 years that charcoal increased in south-west Africa during wetter stages and that a moderately wet climate enabled higher fire activities. We conclude, therefore, that the conditions between 7.1 – 5.8 Ma were significantly wetter than today but drier than before the fire period. As rainfall continued to decrease the grasses retreated and the extreme fire regime ended.

During the fire regime a shift in the isotopic carbon composition is recorded which is best explained by a change in the contribution of C₄ plants to the total vegetation. The data suggest a selecting process of C₄ grasses over C₃ grasses by the fires. That fire influences the selection of grasses has been shown in South Africa where one lineage consisting almost exclusively of C₄ grasses is very abundant and diverse in areas with frequent fires (Visser et al., 2012). The fire regime thus had an irreversible impact on the south-west African biomes by establishing C₄ grasses which benefitted afterwards from better competitiveness under arid conditions (e.g. higher water-use efficiency) (Hatch, 1987) and reduced atmospheric CO₂ levels (Ehleringer et al., 1991).

5.3 Aridification and its link to the Benguela Upwelling

In the third manuscript (Chapter IV) the dinoflagellate communities suggest changes in the ocean circulation and upwelling intensity. A weak pressure gradient is suggested for the period prior to 7.8 Ma. A stronger influence of the Angola Current, comparable with Benguela Niño conditions, occurred more regularly in that time period. From 7.8 Ma on, the influence of the Angola Current decreased most probably because of an intensifying meridional pressure gradient. Resulting stronger trade winds also enhanced the upwelling which is recorded as an increase of dinoflagellate cyst accumulation in general and that of heterotrophic species in particular. Within the period from 6.8 to 5.2 Ma the quality of the upwelled water changed which is related to the Messinian Salinity crisis. The varying amount of outflow from the Mediterranean Sea and the closing of the Central American Seaway influenced the North Atlantic deepwater formation (Billups, 2002; Pérez-Asensio et al., 2012) and probably influenced the source water of the Benguela Upwelling System as well. The continuation of the shoaling of Panama and the intensification of the Hadley Circulation further increased the upwelling and therefore the productivity after 4.4 Ma. These stepwise changes correlate well to the development of the vegetation on the continent. In both cases the data suggest a steepening of the meridional pressure gradient resulting into a northwards shift of the Angola-Benguela Front reflected by the dinoflagellate cyst assemblage changes and a decrease of humidity on the continent reflected by the vegetation changes.
5.4 Outlook

The suggested role of fire as a driver of the C$_4$ grassland expansion is to be further tested in other regions were they dominate today such as East Africa and South America. The combination of pollen, microscopic charcoal and stable isotope analysis might also reveal the role of fire in the expansion of East African savannah, which is of special interest regarding hominine evolution e.g. the development of bipedalism (Cerling et al., 2011). A pollen and charcoal record from sediments of the Niger Delta (Morley & Richards, 1993) already suggested that there are links between fire and grassland expansion in West Africa. A combination of stable isotope analysis and pollen analysis might reveal insights in the contribution of C$_4$ grasses and reveal if they are here favoured by fires, too. In north-east Africa a study of pollen and carbon isotope data shows that the savannah grassland expansion in that region is independent from the C$_4$ grass contribution (Feakins et al., 2013). Hence, a re-analysis of these data considering the microscopic charcoal might resolve a similar pattern in relation to fire as for the current study.

The results of this thesis provide more details about the meridional thermal/pressure gradient during the Late Miocene and Early Pliocene in south-west Africa, which region has been sparsely covered so far and could, therefore, help to improve earth system models of the Mio-/Pliocene. Additionally, since fire is an important driver in grassland expansion it should be considered in vegetation models, especially because it might give indications about seasonality contrasts.

5.5 References


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Sebastian Hötzzel