Sudanian versus Zambezian woodlands of Africa: Composition, ecology, biogeography and use

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Highlights

- Continental break-up and land use change explain the vegetation differences between Sudanian and Zambezian regions.
- The most drastic land use change is the conversion of woodlands to arable land.
- Resource use need to be managed sustainably.
- Maintain the balance between woodland use and it capacity to recover from change is crucial.

Abstract

The Sudanian woodlands (SW) and Zambezian woodlands (ZW) of Africa cover two extensive vegetation zones in Africa. The main question is how similar or different are their woodlands. This paper aims to synthesize available information on woodlands of the Sudanian (SR) and Zambezian (ZR) regions in terms of: i) their floristics and ecology, ii) main drivers of change, iii) their socio-economic relevance to local populations, and iv) how resource use affects the main drivers.

This synthesis deals with 141 publications, including 94% research articles and books on Sudanian and Zambezian woodlands of Africa. Google Scholar's search engine were used. Inclusion criteria comprised the geographical focus (Sudanian and Zambezian regions), the ecosystem type (woodland), and the type of information reported in the studies (ecology, socio-economic and biogeography aspects). The overall results were categorized as addressing either ecological or socio-economic aspects of woodlands.

The SW and ZW share a number of families, genera and species. The ZR counts at least 8500 plant species, of which 54% are endemic, while there are possibly no more than 2750 plant species in the SR. Three distinct woodland types are ecologically important and clearly differentiated in the ZW. However, combined effect of the wide tolerances of the species and the gradual change in the climate in the SZ, makes it difficult to recognize distinct woodland systems. The presence of great rifts and swells in the Zambezian part of Africa, explain in part the difference in the vegetation composition and the high diversity and plant endemism in the Zambezian zones. In both Regions, use of woodland and the associated ecological impacts are quite similar.

Both biogeography and land use change explain the vegetation differences between the two regions. Knowledge of factors underlying vegetation adaptations and change provide a basis for sustainable resource use through integrated multiple-use systems.

Keywords: African rifting; Biogeography; Ecology; Woodland; Sudanian region; Zambezian region

1. Introduction

The vegetation in Africa varies from tropical moist forests to deserts. The macro-ecosystems of Africa, especially phytochoria, are among the richest of the Biosphere in terms of diversity in plant species. It is one of the world's biodiversity hotspots (Poorter, 2004). However, loss of tree cover is considered as one of the main factors contributing to change in climate worldwide. African vegetation, in the global context, is facing the negative impacts of global change (population growth with related climate and land use change), and such change is perceived to be more pronounced in the Sudanian and Zambezian Regions of Africa (Walker et al., 1999).

The Sudanian and Zambezian woodlands are part of the two major phytochoria of Africa (Fig. 1) (White, 1983; Geldenhuys and Golding, 2008). These two extensive vegetation zones are the most prominent terrestrial ecosystems of Africa, covering 17.3 million km^2 in 74% of 41 Sub-Saharan African countries (Geldenhuys and Golding, 2008). They provide a wide range of goods and services to local populations. However, the ongoing changes in their ecosystems, as a result of unsustainable resource use practices over centuries to millennia, are continuously being highlighted, and is a concern for many ecologists. People have transformed the vegetation by altering the distribution of valuable indigenous tree species, increasing the extent of farm fields and fallows (Devineau, 2001; Toledo and Salick, 2006). Human alteration of plant distribution and abundance is known to result from complex interactions of biophysical and sociocultural systems (Robbins, 2004).

Several studies in both Sudanian and Zambezian Regions focused on the ecology and use of the plant species and systems to sustain the ecological processes (Syampungani et al., 2011, 2016; Assédé et al., 2012b; Kalaba et al., 2013; Chichinye et al., 2019). Often there are conflicting views on sustainable socio-economic development needs for sustainable rural livelihoods, commercial interventions, climate change mitigation and environmental conservation, because of the different perceptions of scientists, resource use managers and the policies on the sustainable resource use practices (Syampungani et al., 2011; Kalaba et al., 2013). The prominence of woodlands in rural societies' livelihoods, especially in Africa, requires working towards sustainable integrated, multiple-use resource use management systems. However, the main question is to what extent are the Sudanian and Zambezian woodlands similar or different in terms of vegetation patterns (composition, structure and ecology) in order to consider applying the same or different resource use management interventions? Both the Sudanian and Zambezian vegetation are defined as warm, seasonally dry and fire-prone woodlands. So the main questions that arise are: i) what are the factors that would explain the similarities and differences in species composition, and ii) why is there a total absence of single-species dominance vegetation in the Sudanian Region as it is in the Zambezian Region, for example Mopane woodland? A critical analysis of the biogeographical history of Sudanian (mainly Sudanian *Isoberlinia* and Undifferentiated woodland) and Zambezian (mainly Miombo woodland dominated by *Brachystegia* and *Julbernardia*, Mopane woodland and Undifferentiated woodland) regions can provide the first step to answer these questions. The general hypothesis is therefore that the presence of the escarpments resulting from the continental break-up and the tectonic activities that created the great rift valleys and the associated soil types, explain the vegetation differences between the Sudanian and Zambezian regions (Baker and Wohlenberg, 1971; Partridge, 1987; Burke and Gunnell, 2008). A synthesis of the available ecological information, for instance, on how the rift valley affected the two systems, can be the basis for understanding the relationship between the two Regions.

Since in their respective Regions, the Sudanian and Zambezian systems are contiguous over wide areas in the same latitudes, respectively north and south of the equator, the coexistence of similar vegetation types can be expected. But the sharing of some plant species and the existence of different plant species between the two Regions require explanation. We aim to provide a better understanding of the ecology of Sudanian and Zambezian woodlands, including their biodiversity and the role of their main ecological disturbances. Under the scenario described above, the second aspect to be analysed in this paper is the comparative socio-economic relevance of the two vegetation systems and their plant species to local populations and the main anthropogenic drivers of vegetation change in the Sudanian and Zambezian Regions. In general, we hypothesized that there is no similarity between Sudanian and Zambezian woodlands in terms of ecology and main drivers of change, primarily because of landscape differences. To analyse main drivers of woodland change, we also assumed that the existing land use systems are not aligned with sustainable development at rural household level.

2. Materials and methods

This synthesis deals mainly with literature on Sudanian and Zambezian woodlands of Africa. We used Google Scholar's search engine between June 2016 and January 2018 to identify the literature on Sudanian and Zambezian woodlands of Africa Younger (2010); Halevi et al. (2017). The search results were further screened based on titles, keywords and abstracts to identify the most relevant publications on the woodlands. Inclusion criteria comprised the geographical focus (Sudanian and Zambezian regions), the ecosystem type (woodland), the publication's language (English and French) and the type of information reported in the studies (biogeography, ecology and socioeconomic aspects). We also assessed the reference lists included in the selected publications for additional potentially relevant literature. The overall results were recorded and categorized by hand as addressing either ecological, economic and/or social aspects of woodlands.

Within the ecological category we were interested in vegetation structure, floristic composition (similarities and differences between the two regions in terms of families, genera and species, including endemics), historical vegetation changes and potential drivers of vegetation dynamics (climate, soil properties, topography, as well as natural and anthropogenic disturbances). Vegetation structure included information about vegetation physiognomy, vegetation layers, tree and herbaceous cover. Regarding species composition, liana, bryophyte and fungal species were not included although they could be interesting discriminant factors. Economic and social aspects of woodlands encompass mainly the resource use by local populations, in both Sudanian and Zambezian woodlands of Africa. We eventually selected 141 publications, including 80% research articles, 14% books and 6% reports (grey literature) from the retrieved literature. The selected literature encompasses a 87-year period, starting from 1932 to 2019. The majority of the articles focused on Sudanian

(36%) and Zambezian (35%) woodland composition, structure, use and drivers of change, while only 17% articles reported on the biogeography of Africa.

3. Results and discussion

3.1. Floristic composition and associated characteristics as pattern of similarities and differences between the two regions

The similarity between some components of the Sudanian woodland (SW) and Zambezian woodland (ZW) was highlighted by White (1983) and Timberlake et al. (2010). In the ZW, three distinct woodland types are ecologically important and clearly differentiated because of their floristic and substrate differences, but also because of their widespread socio-economic importance: Miombo woodland (MiW), Zambezian Undifferentiated woodland (ZUW) and Mopane woodland (MoW). In the SW, the combined effect of the wide tolerances of the species and the gradual change in the climate, renders it difficult to recognize distinct zones and distinct vegetation types. Nevertheless, two main woodland types can be differentiated: Sudanian Isoberlinia Woodland (SIW) and Sudanian Undifferentiated Woodland (SUW).

3.1.1. An overview of species composition

From White (1983), large differences appeared between species composition of Sudanian Region (SR) and Zambezian Region (ZR). The ZR counts at least 8500 plant species, of which 54% are endemic, while there are possibly no more than 2750 plant species in SR. The ZR has a richer flora and three times as many endemics as the SR. While there are no endemic families in both Regions, the ZR presents some woody endemic genera, including *Colophospermum* and *Diplorhynchus*. However, few endemic genera (*Pseudocedrela*, *Vitellaria* and *Haematostaphis*) were reported for the SR (White, 1983). All endemic genera of either SR or ZR are monotypic. While most of Zambezian species are really specific to the region and localized, a high proportion of Sudanian linking species are widespread in the moderately dry parts of Africa and many extend to other parts of the tropics. The two Regions share a number of families, genera and plant species, mostly from the Caesalpinioideae subfamily (Frost, 1996). The relations between the woodlands of the two Regions were asymmetric because, in the SR, 46% of the species are shared with the ZR, whereas in the ZR, only 24% of the species are shared with the SR. Basically they share the same number of species, but because the ZR has a higher total number of genera and species, the percentages are lower. *Piliostigma thonningii*, *Parinari curatellifolia*, *Dalbergia melanoxylon* and *Burkea africana* are four of the shared tree species between the two regions. Plant species show an appreciable interval between their Zambezian and Sudanian areas. In general, the herbaceous and small woody species of ZR showed a similar relationship to the Sudanian Region as do the trees, but it is less well-defined since a higher proportion of herbaceous species also extend to more distant phytochoria. The differences in species composition are more pronounced when the woodland types within and between regions are compared.

These relations are understandable on the basis of the general trend towards aridity during the Miocene and later. The Sudanian Region is much drier than the Zambezian Region. Its greater aridity has no doubt been the crucial factor in impoverishment of its flora, and in the asymmetry of savanna-type vegetation depicted on many vegetation maps (Axelrod and Raven, 1978).

3.1.2. Miombo and Sudanian Isoberlinia woodland

Miombo (MiW) and Sudanian Isoberlinia woodlands (SIW) are both dominated by Fabaceae and Poaceae plant families. A comprehensive list of woody species of MiW and SIW was not available. Contrary to Miombo, several sub-units were described for SIW in previous studies (Houinato and Lejoly, 2001; Kakaï and Sinsin, 2009; Nacoulma, 2012).

In MiW, 19 tree species of *Brachystegia* and related genera (*Julbernardia globiflora*, *J. paniculata* and *Isoberlinia angolensis*) are dominants. SIW is only dominated by *Isoberlinia doka* and *I. tomentosa* with some associated species such as *Afzelia africana*, *Anogeissus leiocarpa, Combretum micranthum, C. nigricans, C. glutinosum*, *Manilkara multinervis*, *Monotes kestingii*, *Terminalia avicennioides*, *Uapaca togoensis* (Houinato and Lejoly, 2001; Kakaï and Sinsin, 2009). The *Brachystegia/Julbernardia/Isoberlinia* canopy dominants of Miombo are extremely gregarious, which allow only a few other species to enter the canopy. The principal canopy associates are *Afzelia quanzensis*, *Anisophyllea pomifera*, *Erythrophleum africanum, Faurea saligna*, *Marquesia macroura*, *Parinari curatellifolia*, *Pericopsis angolensis* and *Pterocarpus angolensis*. In addition, *Uapaca* and *Monotes*, typical SIW species, do occur scattered in Miombo woodland as small trees less than 10 m tall. *Isoberlinia* spp also are described as gregarious species (Kakaï and Sinsin, 2009; Goussanou et al., 2017) in SIW, but not as pure stands as with Miombo dominants. Lianes, pteridophytes, and bryophytes are normally absent from both SIW and MiW, except on fire-protected sites, rocky places, termite mounds, and in secondary Miombo.

3.1.3. Zambezian and Sudanian undifferentiated woodland

Undifferentiated woodlands are the richest woodland types sharing several species from Sudanian Isoberlinia woodland to Miombo woodland. There are several sub-units in both Regions because of absence of clear dominants. The term undifferenciated woodland is not properly used in SR, probably because of the phytosociology methods (Braun-Blanquet, 1932) used to study the vegetation based on the partitioning of vegetation into small units defining the association concept (White, 1983; Sinsin, 1994; Nacoulma, 2012). However, some dominants were defined for the identified plant communities or associations. Past and recent studies in SR (White, 1983; Sinsin, 1994; Houinato and Lejoly, 2001; Ouédraogo, 2009; Nacoulma, 2012; Assédé, 2014) converged with floristical components of the identified sub-units. The latter are mainly dominated by Combretaceae (*Anogeissus leiocarpa*, *Combretum glutinosum, C. nigricans, C. micranthum, Terminalia avicennioides*), Fabaceae (*Acacia gourmaensis*, *A. hockii*, *A. dudgeoni*, *A. seyal*, *A. sieberiana*, *Acacia macrostachya*) and other species like *Vitellaria paradoxa*, *Parkia biglobosa*, *Piliostigma thonningii*, and *Feretia apodanthera*.

In ZR, some sub-units are defined as undifferentiated woodlands (White, 1983; Werger, 1978a; Werger and Coetzee, 1978; Skarpe, 1986; Childes and Walker, 1987, Skarpe, 1990). The important part in terms of tree cover is the zone in southern part of Angola and Zambia, northern parts of Namibia and Botswana, and western part of Zimbabwe, dominated by *Baikiaea plurijuga*, *Guibourtia coleosperma*, and *Pterocarpus angolensis* (Skarpe, 1990; Chichinye et al., 2019). Extensive areas of Undifferentiated woodland in ZR, further south, do not have *B. plurijuga* or *G. coleosperma*, and *P. angolensis* occurs only in some areas. A critical analysis of the two vegetation types between SR and ZR shows a replacement of some tree species between Regions. *Terminalia sericea*, *Pterocarpus angolensis* and

Philenoptera violacea of ZUW are replaced by *T. avicennioides*, *P. erinaceus* and *P. laxiflora* respectively, in the SUW.

3.1.4. Mopane woodland

The main characteristic is a total dominance of *Colophospermum mopane*. The species composition of the Mopane woodland varied with the development stage. In the tall mopane in the Luangwa Valley (Chidumayo and Marunda, 2010), the most conspicuous associates are *Acacia nigrescens*, *Adansonia digitata*, *Combretum imberbe*, *Sclerocarya birrea* and *Kirkia acuminata*. *Colophospermum mopane* and the miombo dominants scarcely occur together and their associated floras are almost totally dissimilar. Even if found adjacent to Miombo woodland or low woodland dominated by *Combretum* or *Terminalia* species, there is little overlap in species composition between the three types, with the mopane vegetation generally having fewer species and a poorly-developed grass layer.

3.2. Vegetation attributes

Woodland is the most widespread and characteristic vegetation of the surviving natural and semi-natural stands in both Zambezian and Sudanian Regions (Geldenhuys and Golding, 2008). The vegetation cover is an open canopy of trees and shrubs with an understory characterized by herbaceous vegetation (White, 1983). Contrary to Zambezian Region, there is virtually no true forest in Sudanian Regions (Trochain, 1940; Aubréville, 1950; Diatta and Grouzis, 1998). Vegetation structure vary with woodland type.

3.2.1. Miombo and Sudanian Isoberlinia woodland

Termed rightly or wrongly Sudanian Miombo (Keay, 1951; Timberlake et al., 2010), Sudanian Isoberlinia woodland (SIW) can be regarded floristically as an impoverished variant of Miombo woodland (MiW). *Brachystegia* and *Julbernardia*, the two most characteristic genera of MiW, were replaced by *Isoberlinia*, *Monotes* and *Uapaca* in SIW. Contrary to MiW, the canopy in SIW is scarcely more than 15 m tall with few or no understorey tree species. Very few Miombo species are represented (Aubréville, 1937, 1950; Kokou et al., 2006; Assédé, 2014). Three layers can be distinguished for both MiW and SIW. In SIW, the general woody cover is over 50% (Houinato and Lejoly, 2001; Nacoulma, 2012) and the herbaceous cover is dominated by tall, more or less shade-tolerant, perennial grasses, such as *Andropogon tectorum* and *Pennisetum unisetum* (Houinato and Lejoly, 2001; Oumorou and Lejoly, 2003; Ouédraogo, 2006; Nacoulma, 2012). Compared with the SIW, the MiW exhibits a more complex structure and phenology, probably as a consequence of the mixed influence of more varied rainfall, lower temperature, and complex soil patterning (Davis, 2011). It is characterized by a relatively dense woody understory. However, this very much depends on the fire regime and development stage of recovery after major changes. Annual early dry season fires and exclusion of fire can result in a woody understory in Undifferentiated woodland, while annual late dry season fires result in an open grassy understory (Geldenhuys, 1977). These patterns have been observed in both Miombo and Mopane woodlands (Geldenhuys, 1977; Geldenhuys et al., 2017). The aggregated distribution of both MiW and SIW tree species probably resulted from the main dispersal mode of the tree species which consisted of dropping the seeds from pods under the mother tree, and root suckering (Ky-Dembele et al., 2007; Kakaï and Sinsin, 2009; Goussanou et al., 2017).

3.2.2. Zambezian and Sudanian undifferentiated woodland

Undifferentiated woodland, both in Zambezian and Sudanian Regions, is a mixed stand of wooded grassland and grassy woodland. They are floristically richer than Miombo, Mopane or Isoberlinia woodland and more easily defined by the absence of the Miombo and Mopane dominants (*Isoberlinia* in Sudanian Region and *Brachystegia* and *Julbernardia* in Zambezian Region) than by their own floristic composition (White, 1983). The transitional nature of the undifferentiated woodland allowed the occurrence of both Miombo and Mopane species in Zambezian Region (ZR) and *Isoberlinia* and other woodland species in Sudanian Region (SR). Compared to ZR, where undifferentiated woodland covers a relatively small area (but still extensive), it is the prevailing vegetation in SR (White, 1983). The structure of this vegetation type was quite similar in the two zones with two layers and a developed understory. However, there are sufficient ecological differences to consider them different. They are both very variable floristically. Several variants of SUW were described with high similarity between the dryland groups in West Africa (Ouédraogo, 2006; Ouédraogo, 2009; Nacoulma, 2012; Assédé, 2014). The boundary between the variants was not always clear. There were considerable floristic overlap between several SUW and variation was more or less continuous. The main differences between them were the dominant tree species (*Anogeissus leiocarpa*, *Combretum spp*, *Terminalia avicennioides*, *Crossopteryx febrifuga*, *Acacia spp*, or *Burkea africana*), the tree cover (20%–75% cover) and the height (12 m–17 m) (Campbell , 1996; Ouédraogo, 2009; Assédé, 2014). The physiognomy of the understory layer was heterogeneous but dominated with a cover of less than 40%. A shrub layer dominated by *Combretum micranthum* or *C. collinum* can be identified with at least a 10% cover. The structure of the herbaceous layer remains homogeneous for the two tree cover types. The probable differences are the dominant herb species (*Hyparrhenia spp*, *Andropogon gayanus*, *A. pseudapricus* and/or *Indigofera pulchra*), the herb cover (40%–65% cover) and the height (2 m–2.5 m). A variant in Senegal, termed Transition Woodland, is characterised by low density (54-118 individuals per ha) with many large trees and a relatively large basal area (8.6–12.8 m^2 per ha) (Lykke and Sambou, 1998).

Various sub-units of ZUW are described in north-western part of Zimbabwe (Childes and Walker, 1987) even if the main physiognomy is defined by *Baikiaea plurijuga* woodlands. The two main vegetation types are woody scrub of *Terminalia sericea-Burkea africana* and *B. plurijuga*-dominated woodlands. Two patterns of structure were described for ZUW: Baikiaea woodland on the dune ridges, surrounded by *Terminalia* mixed scrub, and occasionally *Colophospermum mopane* in the troughs or a mosaic of *Baikiaea* woodland and *Terminalia* scrub (Werger and Coetzee, 1978; Skarpe, 1986; Childes and Walker, 1987). Whatever the pattern, ZUW is defined with two layers: a well-developed tree or shrub layer and a relatively homogeneous and low herb layer. The main differences between the two main vegetation types are the dominant tree species (*Baikiaea plurijuga*, *Terminalia sericea, Guibourtia coleosperma*) and the tree cover (26-39% cover).

3.2.3. Mopane woodland

Mopane woodland communities are dominated by *Colophospermum mopane*, and occur widespread in the drier half of the Zambezian Region (ZR). Mopane woodland is confined to the flora of the ZR and were not found in other parts of Africa or tropics. Homogenous and almost exclusive mopane stands of old stage are sometimes termed “cathedral mopane”. The tallest woodland is 10–20 (25) m height (White, 1983; Timberlake, 1995). Despite the diversity in height and density of Mopane communities, they have a remarkable physiognomic uniformity. The structure of Mopane woodland cannot be compared with any of the Sudanian woodland types due to the almost complete dominance of *C. mopane* itself and its very characteristic appearance. On dry land, no Sudanian tree species develop such monospecific (pure) stands as mopane. Perhaps in wetlands, *Terminalia macroptera* or *Mitragyna inermis* woodlands can sometimes develop pure stands, similar to mopane woodland (Ouédraogo, 2009; Assédé et al., 2012a). However, regardless of their extent and vegetation structure, they are very different. Mopane woodland can cover areas up to 100 ha, and more, with only one tree layer (Mapaure, 1994), while *T. macroptera* or *M. inermis* woodland was found only on less than 1 ha as pure stands (Assédé et al., 2012a). Regardless of tree size, except when damaged, Mopane woodland was usually a single-stemmed tree, or multi-stemmed appearing like clustered. Irregularly deciduous for up to five months, like most dominants of Sudanian woodland, Mopane woodland does not appear to have an analogue in the SW. In some areas, like Zimbabwe and Botswana, there are extensive areas of scrub mopane with no large trees and most of it about 2–3 m tall. The question is: which factors influence the development of scrub mopane? Authors have argued on the frequency of fire to maintain Mopane woodland at scrub stage (Gandiwa and Kativu, 2009). However, grass is sparse or absent in well-developed mature Mopane stands, hence fire-damage is minimal (Kelly and Walker, 1976; Timberlake, 1995).

3.3. Ecology of Sudanian and Zambezian Regions

3.3.1. Climate and soil

Both the Zambezian and Sudanian Regions occur within Walter's tropical summer rainfall zone, with similar climates (White, 1983). The climate in Sudanian and Zambezian woodland is defined as warm dry with a dry season of three months or more (Davis, 2011; Happold and Lock, 2013). The warm mesic Sudanian dry woodlands experience a long wet period of about 4.5 months compared to 4 months in the warm mesic Zambezian dry woodlands. But the range in mean rainfall of 600–1200 mm is similar in the two regions. The main difference is their seasonal separation throughout the year, with clearly different seasons in ZR. However, the temperature in the SR is appreciably higher (mean annual temperature 24-28 °C), and, because of the harmattan wind, the dry season is more severe. Frost in the ZR (Childes and Walker, 1987) is usually observed along open valleys and on the top of highlands (mountains and hills), but is totally absent in the SR.

The soil properties, factors determining the distribution of plant species (Thiombiano et al., 2006), are quite different. Broadleaved woodlands, such as Miombo woodland, Undifferentiated woodland and Isoberlinia woodlands in western SR and ZR tend to occur on similar nutrient-poor soils. Miombo woodland is generally found on lighter-textured, nutrient-poor but well-drained soils on the African Plateau, but Mopane woodland is mostly confined to lower-lying areas with clay and nutrient-rich soils (Timberlake, 1995; Chidumayo and Marunda, 2010). Mopane woodlands occur on heavier-textured soils in the wide, flat valley bottoms of lower-altitude river valleys (Mapaure, 1994), at an elevation of 200–1200 m, but normally in the range of 300–900 m. In Sudanian warm, mesic dry woodland, soils are recent and sometimes with >70% sand (Ouédraogo, 2009; Nacoulma, 2012; Assédé, 2014). Specifically, Undifferentiated Woodland in Zambezian Region (UWZ) cover Kalahari sands. Soils are deep, highly pervious, and fine to medium grained sands to loamy sands, typical group in the amorphic soil order (Nyamapfene, 1991). The underlying geology is of sedimentary rocks overlying Karoo basalt and sedimentary deposits very low in silt (1.09–0.09%), clay (2.65–0.18%) and high dry organic matter (99.8%) (Childes and Walker, 1987).

Undifferentiated woodland in Sudanian Region (SUW) establish on more rich soils. Soils are well drained with neutral (6.9) or weakly acidic (6.4) pH, sandy-loamy and moderately moist (Sinsin, 1994; Houinato and Lejoly, 2001; Ouédraogo, 2009; Nacoulma, 2012; Assédé, 2014).

3.3.2. Natural ecological drivers of vegetation change

The determinant of woodland change in the Sudanian and Zambezian Regions (SZW) is a long-standing question in ecology. Studies have proposed a variety of contributing factors. Some studies linked woodland dynamics with soil and climate limitations (Jobbágy and Jackson, 2000), whereas others attributed differences to fire, browsing and drought (Roques et al., 2001; Bond et al., 2005; Higgins et al., 2007; Sankaran et al., 2008; Staver et al., 2009). From a different point of view, woodland dynamics would be determined by both: the climate and site conditions determine the potential of vegetation cover type in an area, but fire, browsing and drought/floods change the potential into the reality in terms of vegetation dynamics. This vegetation change can be read through change in stand development stages of the same vegetation system, from wooded grassland to closed woodland and vice versa, and/or plant composition and productivity.

Fire has been burning ecosystems for millions of years, defining the actual distribution of global biomes. It assures and maintains the structure and function of fire-prone communities like Sudano-Zambezian Woodlands (SZW). Changes in fire regimes affect species composition (Geldenhuys, 1977; Uys et al., 2004), vegetation structure and functioning, with cooler fires during the early dry season, resulting in an increase in fire intolerant species and a total biome shift. In fire-prone ecosystems, the most affected by fire suppression are seedlings and plants with high light demands (Leach and Givnish, 1996; Uys et al., 2004). Woody encroachment and forest invasion in vegetation like SZW were always defined as attributes of fire exclusion from a flammable system (Swaine et al., 1992; Bond et al., 2005). As in mesic savannas, fire is the main factor maintaining SZW. Modification in fire regimes of frequency, intensity, season, and extent can trigger rapid woodland change because different fire regimes produce different landscape patterning. In contrast to animals, fire is a non-selective browser, and plant species respond to fire from their own adaptations. Animals and people are selective browsers, and would have a different effect.

One of the bio-indicators of woodland change are geoxyle plants. Such stands are rightly or wrongly called African underground forest ecosystems, and occur in SZW as a bio-indicator, characterized by greater fire frequency (White, 1977; Maurin et al., 2014). Change in geoxyle plant occurrence can be read as a starting point of vegetation change. As important biological components of woodlands, termites and large herbivores, influence the vegetation (Holdo, 2007; Mapaure and Moe, 2009; Aarrestad et al., 2011; Kassa et al., 2014; Scogings, 2014; Acanakwo et al., 2017). Increase in herbivore numbers would increase pressure on the vegetation through browsing, branch-breaking and ringbarking, with plant species best able to compete for resources, shifting to those tolerant of herbivory (Hairston et al., 1960). However, exclusion of large herbivores would negatively impact on, for example, their role as seed dispersal agents or inducer of early budding of *C. mopane* in Zambezian Regions (Styles and Skinner, 2000; Keesing and Young, 2014).

Several studies reported that climate change would impact woodland dynamics. The question is in which direction. The studies of Houérou (1996) and Cauwer et al. (2016) demonstrated the negative impact of climate change on woodland vegetation. Predictions suggested that undifferentiated woodland can expect pronounced impact of climate change through drought with important reduction of woody cover (Sankaran et al., 2005, 2008). Increasing aridity, reported to explain the spread of grasses, is one potential pathway to woodland change (Strömberg, 2011). These negative effects were moderated by the reported "greening up" trend in Sudano-Sahelian Region (Anyamba and Tucker, 2005; Heumann et al., 2007). However, subsequent studies did not support this idea because the greening trend of Sudanian woodland, reported over the past 25 years with Remote Sensing based analyses, revealed great impoverishment on the ground of the woody vegetation cover (Herrmann and Tappan, 2013). Studies also agree that woodland change is influenced by more than one factor. The question is how can the effects of climate change be evaluated in addition to the effects of change in other factors, such as land use and resource use practices, and fire regimes? The boundary is not always clearly highlighted. Less concrete proofs of changes have been published in Sudanian and Zambezian woodlands. The studies have not yet been able to separate, "on the ground", the relative effect of climate change versus the effect of land use change. Only very few investigations exist on vegetation dynamics, climate change and land use change for the Sudanian zone (Wittig et al., 2007; Bégué et al., 2011; Cauwer et al., 2016). Further analysis could suggest that such behavior is genetically fixed in different plant species.

In an experimental annual burn study in Zambezian undifferentiated woodland in northern Namibia, controlled for substrate and climate variation over a 12-year period, a woody understory developed with cooler early dry season or absence of fire, whereas a grassy understory developed with annual late dry season fires (Geldenhuys, 1977). The rapid vegetative regrowth in Miombo and Sudanian woodland observed by Geldenhuys et al. (2017) and Assédé et al. (2018) is further support of the much bigger impact of land use change, rather than climate change, on vegetation dynamics influencing the woody vegetation.

Obviously, there is a cyclic occurrence of severe droughts, or severe frost, or very extreme fire events, in several parts of the Sudanian and Zambezian woodlands, but such extreme events are part of cycles within cycles of climatic fluctuation, relating to the historical biogeography of the area – not necessarily by what is now considered as a human-induced climate change event. The lack of information hampers the development of adaptive forest and land use management strategies to climate change. Notwithstanding, monitoring forest composition in transition zones can provide an early warning system for climate change impacts.

3.4. Biogeography of Sudanian and Zambezian zones: influence of the African rifting and climate on the vegetation dynamic

3.4.1. Localisation

The Sudanian and Zambezian Region of approximately the same area (respectively 3 731 000 km^2 and 3 770 000 km^2) are distributed differently (Fig. 1) (White, 1983). The Sudanian Region extends across Africa from the coast of Senegal to the foothills of the Ethiopian Highlands between the tropical moist forest zone in the south and the Sahelian domain in the north, with transitions in both directions. It is mostly between 500 and 700 km wide (White, 1983), i.e. a relatively narrow latitudinal zone, which is narrower in the west and broader in the east. The Zambezian Region stretches from the Atlantic Ocean to the Indian Ocean, in a relatively broad latitudinal zone and a narrower longitudinal zone (White, 1983; Timberlake and Chidumayo, 2011). The Sudanian zone falls within the Low Africa sedimentary basins and upland plains, mostly between 150 and 600 m above sea-level. Some isolated highlands over 1000 m above sea-level occur in Niger, Nigeria and Sudan. Most of the Zambezian Region is part of the Great African Plateau, or High Africa, the largest in the world, and rises over 900 m above sea-level, with some lowlands in Mozambique and relatively narrow coastal plains and valley strips elsewhere. The most striking feature of the relief of High Africa is the rift-valley system (White, 1983).

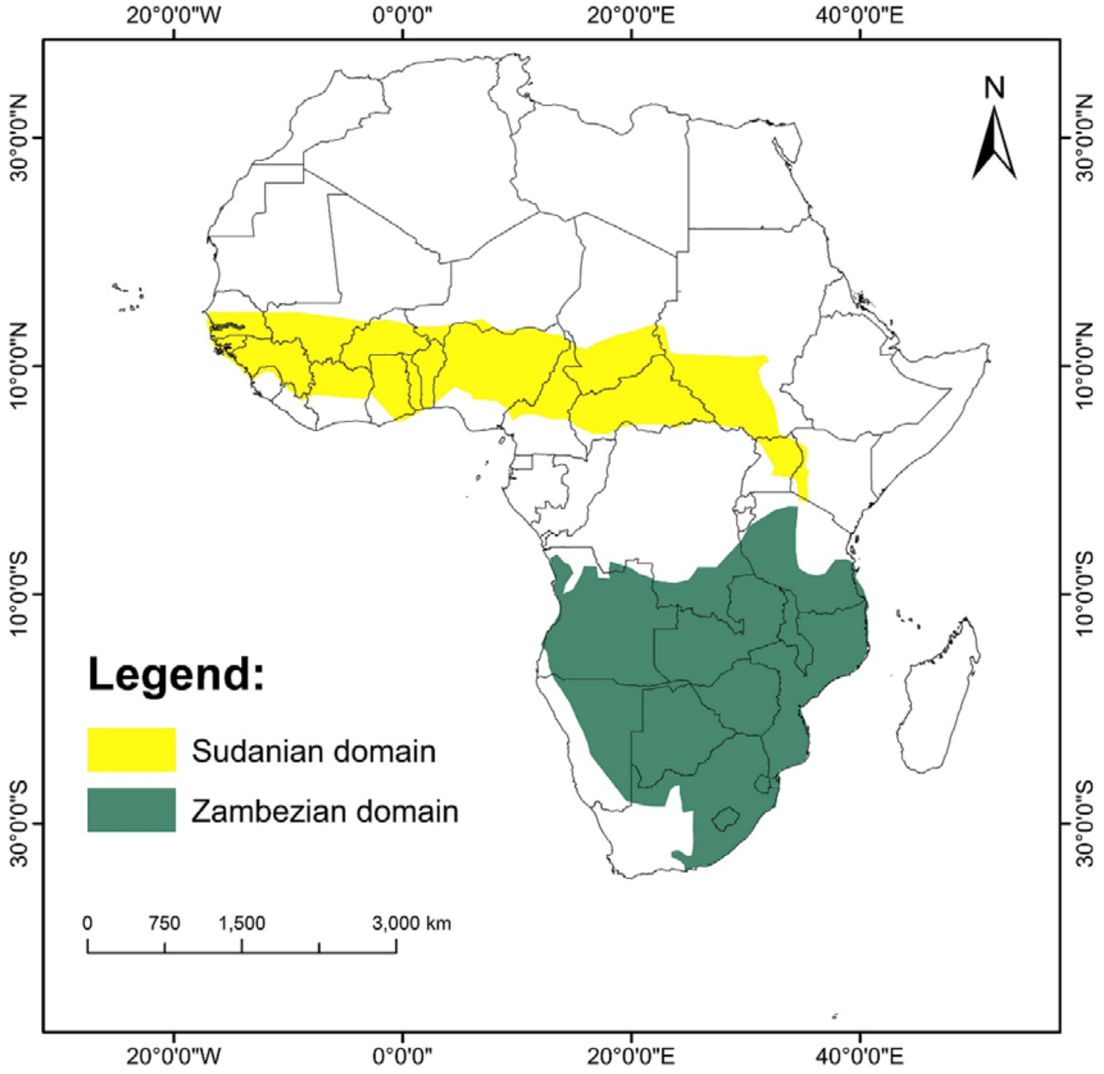

Fig. 1. Sudanian and Zambezian regions in Africa.

3.4.2. Influence of Africa uplift in Sudanian and Zambezian Regions

During the Early Mesozoic time period (245 Ma), Gondwanaland had a low relief (King, 1967), composed of broad plains and basins, and scattered Precambrian (4 Ga) highs. The topography was flat with a high sea level. Most of the existing rift basins experienced marine incursions during late Cretaceous (100–65 Ma) at the end of Mesozoic. Much of Africa, including the Sudanian and Zambezian Regions, was temporary flooded. However, sea level began to subside during the Paleocene (from 65 Ma) (Haq et al., 1987). The tectonic deformations, which occurred as swell uplift and the local rift-flank uplift in East Africa, especially in the Zambezian Region in post-Eocene (from 34 Ma), modified the surface, which presently is higher above sea level than it was during most of its erosional period. Two phases of uplift were assumed (Partridge, 1987) during the past 20 Ma: 150–300 m elevation during the early Miocene (soon after 22.5 Ma) and an additional increment of 900 m since ca. 5 Ma. By the end of the Miocene (5.3 Ma), Africa was uplifted, especially in the East African Zambezian Region, with modification of the soil, relief, and the vegetation. Great escarpments were formed because of the rifts with swells. They contributed to the modification of the surface of the Zambezian Region and probably influenced the vegetation type and plant species composition more, compared to the Sudanian zone. Major uplifts were reported by Baker and Wohlenberg (1971) during the end of the Pliocene-early Pleistocene (5–10 Ma). The interior plateaux were raised more than 1,800 m above the Miocene level. They also steepened the coastal monoclines by hundreds of meters (Toit, 1954). At the same time, the great rift valleys developed in phases (Baker and Wohlenberg, 1971), and new high volcanos were built upon their margins from Ethiopia to Mozambique, through Malawi. It is a key starting point of modification of the actual vegetation in the Zambezian Region. The question is whether that possibly contributed to the differentiation of the African broad-leafed woodlands, into the Sudanian Region and the Zambezian Region, with greater differentiation (speciation) in the Zambezian Region because of the more varied substrates.

3.4.3. Shifts in climate and vegetation of Sudanian and Zambezian Regions: Influence of the rift systems

After the separation of Laurasia from South America, a lowland rainforest was formed in all of the northern part of Africa (Axelrod and Raven, 1978), including the area of the current Sudanian Region, until Late Cretaceous-Paleocene (75-55 Ma). The Zambezian Region in East Africa, at that time, was covered by subtropical rainforest (Fig. 2a). However, during the middle Miocene (16–14 Ma), the movements that brought northeast Afro Arabia against south-central Asia, closed the Tethys Sea (Harzhauser et al., 2007). In the same way, the long-persistent latitudinal circulation system ended (Shevenell et al., 2004; Holbourn et al., 2013). A warm moist climate was brought into the entire Mediterranean region and southern Asia (Zachos et al., 2001). This warm moist climate progressively became drier, especially over northern Africa, including the Sudanian Region, and changed the rainforest into savanna and woodland (Fig. 2b and c) (Burke and Gunnell, 2008). The absence of some Zambezian genera from the Sudanian zone can be explained by the fact that they originally came from the affinity between Australia and the southern part of Africa. This is the case of Podocarpaceae and Nothofagus (evergreen forest components), common to Australia and the Zambezian Region, but absent in the Sudanian Region.

During the Paleogene (66–23.03 Ma), the swells in East and Southeast Africa, including the entire Zambezian Region where the rift system developed (Fig. 3), probably were sufficiently high and cool to enable certain subtropical rainforest taxa, present until late Paleocene, to radiate upward into a temperate montane zone, and presumably also for north temperate and south temperate plants to extend their ranges towards the equator. Dry woodland and scrub observed in the Zambezian Region probably originated early in southwestern Africa, wherever dry sites were available during the late Cretaceous-Paleocene (75-55 Ma). All of these factors, in combination, can explain the high plant diversity of the Zambezian Region, when compared with the Sudanian Region, where the plant diversity was more reduced after the warm moist climate of the Miocene.

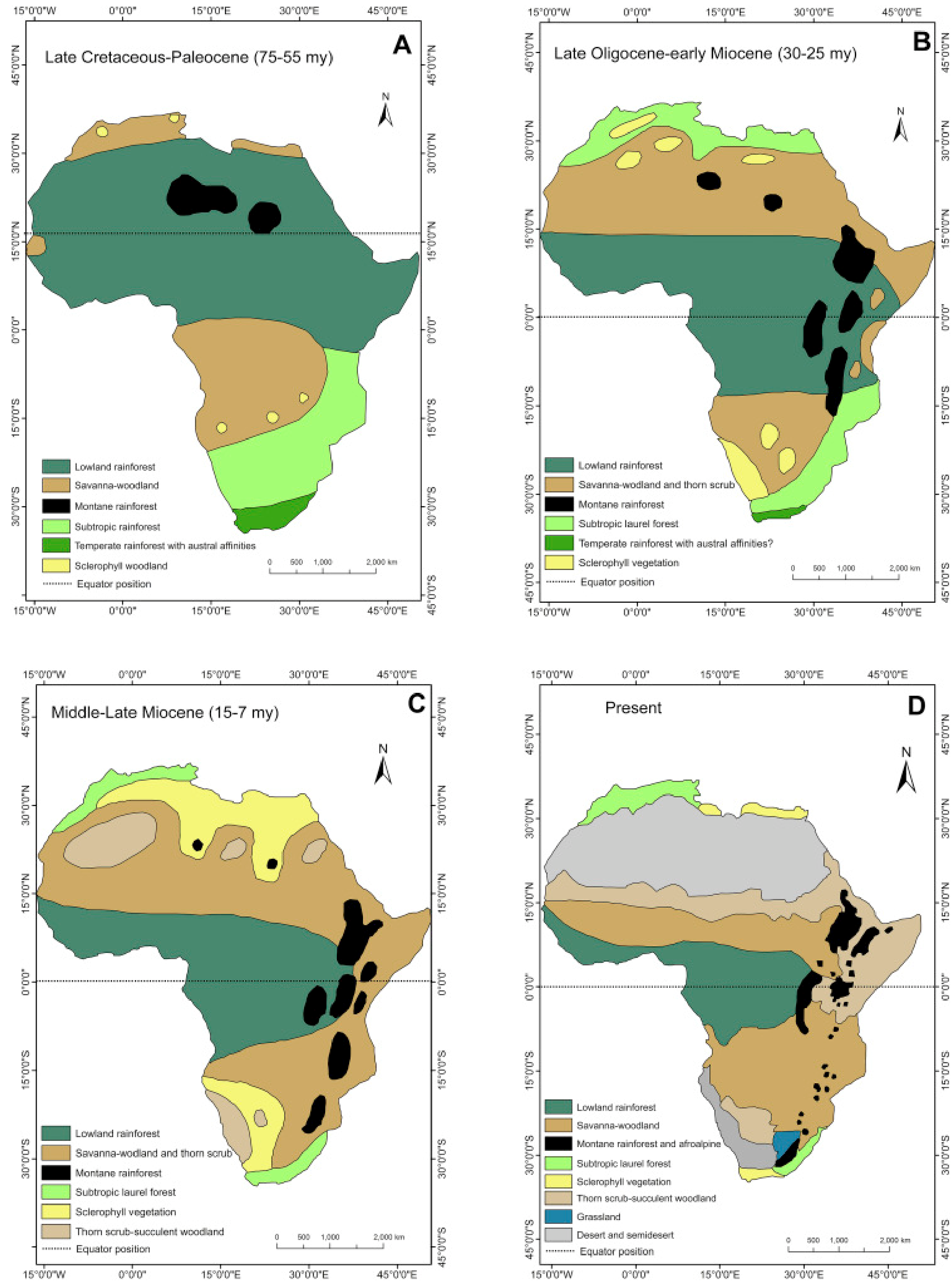

Fig. 2. Evolution in the distribution of the African vegetation. a. Late Cretaceous-Paleocene. b. Late Oligocene-early Miocene. c. Middle-Late Miocene. d. Recent. Modified from Werger (1978).

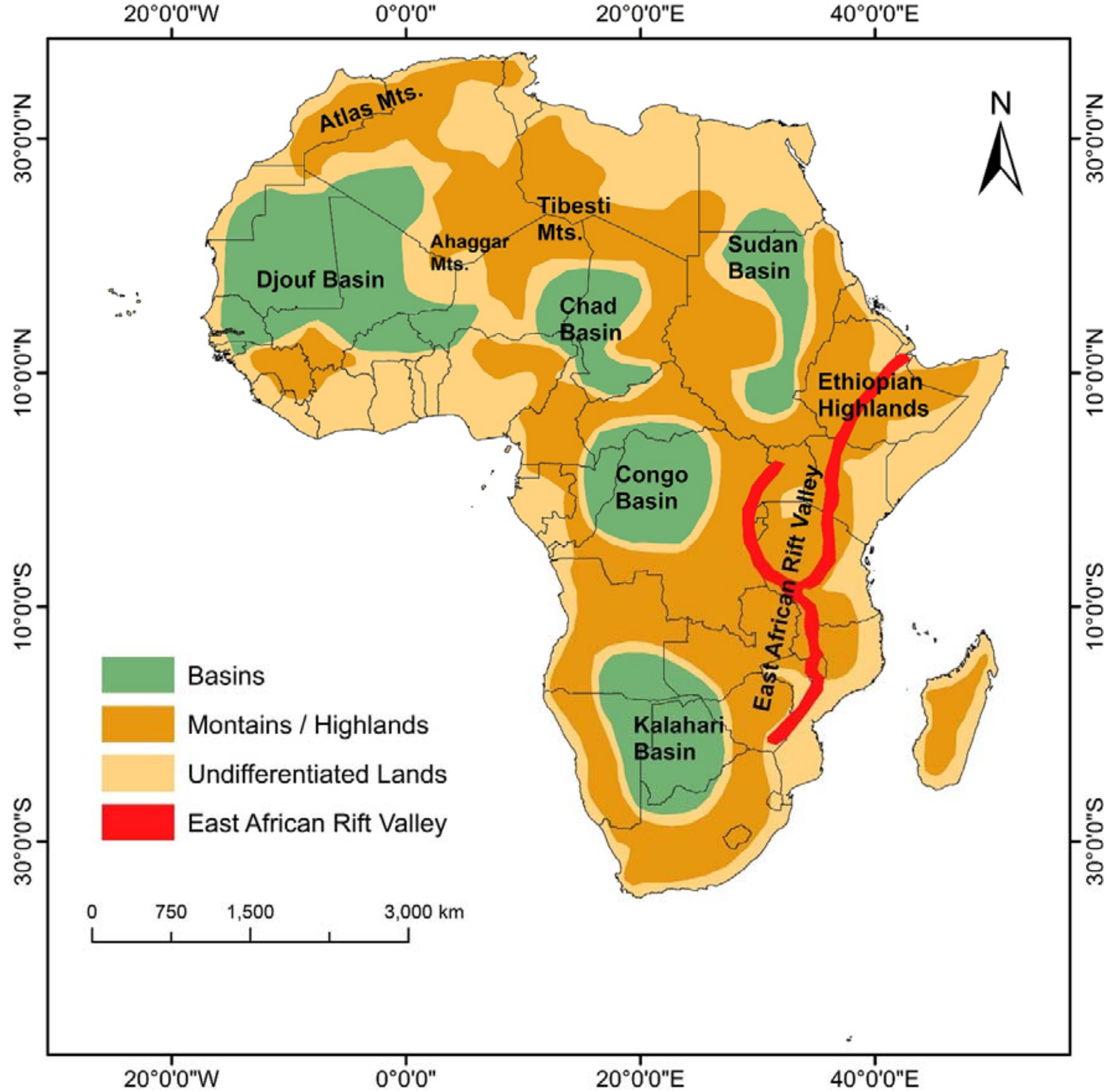

Fig. 3. African rifts and basins during the Tertiary (66 - 258 Ma), (modified from Coussement, 1995).

The modern plant communities arose as climates gradually changed, and especially rapidly in the later Pliocene and Pleistocene (5–1.5 Ma). The African landscape was flexed into a number of broad warps and basins (Fig. 3) during the middle Tertiary (Toit, 1954; King, 1967; Burke and Gunnell, 2008) under the great rift system and volcanism. Late Tertiary (7-5 Ma) woodland, grassland and thorn scrub vegetation in northern Africa, south and southeast Africa, commenced to spread in their areas previously being occupied by rainforest (Fig. 2a and b). Semi desert taxa have in large measure been derived by adaptation of taxa in woodland, savanna and thorn scrub vegetation to the somewhat drier conditions (≤250 mm) that developed over the areas of their former occurrence (Axelrod, 1958, 1970; Axelrod and Raven, 1978), flanking the rainforest over the interior with spreading dry climate. The Neogene (23.03–2.58 Ma) trend towards drier climates, brought on by the general uplift of the continent, changes in circulation, and the resultant decrease in moisture, caused closed forests to retreat as savannas and woodlands replaced them (Fig. 2d). In the Sudanian Region, savannas attained a progressively wider area as the trend towards aridity increased during the Neogene. Many other trees and shrubs of the East African montane forests must have disappeared as precipitation was lowered following the Miocene (23.03–5.33 Ma). This may have contributed to the marked differences in the present woodlands between the Sudanian and Zambezian floristic regions.

3.5. Resource use and drivers of vegetation change

3.5.1. Uses by local populations

The changes in climate, landscapes, and substrates in different parts of Africa resulted in adaptations of plant species to survive under the diverse disturbances. Human disturbances, through various land use practices, are in many ways within the adapted tolerances of species to the natural processes of change (Geldenhuys, 2011). The woodland physiognomy in the Sudanian and Zambezian Regions was also derived from human-induced disturbances. Around 80% of the rural population in both Sudanian and Zambezian Regions relies on woodlands for their livelihoods (Vodouhê et al., 2009; Syampungani et al., 2011; Chirwa et al., 2014). The use of woodlands is very similar between the Sudanian and Zambezian Regions. Studies from different times and areas in the two regions came to the same results in terms of use of woodland by local populations. Traditionally, the land use patterns were more extensive including shifting cultivation or slash-and-burn agriculture. Agriculture in the Sudanian and Zambezian Regions is characterised by burning cleared trees, followed by the rotation of farming and fallow periods (Foumier et al., 2001; Eriksen, 2007; N'Dja et al., 2008). This traditional farming system was adopted in the prospect of preserving soil health and quality. According to Foumier et al. (2001), its success until recently can be explained by the low demographic pressure.

Timber harvesting from woodlands represents direct inputs to satisfy household needs for food, medicine, and materials for construction, and is often the only means for forest dwellers to enter a cash economy (Vodouhê et al., 2009, 2011). Woodlands also offer bulk of fodder for vast livestock, fuel wood for drying major agricultural crops and fish, construction material for homes and fences in both rural and urban areas, precious woods, raw materials for packaging the wares used in homes and in harvesting farm produce. Important non-timber forest products (NTFPs), such as medicines and other foods (Geldenhuys, 2011), are derived from woodland. Construction material and fuel wood uses form a permanent element of the local economy. Fruits and other woodland products harvested during times of shortage, are used intermittently. In Sudanian zone of Republic of Benin, bark harvesting represents 10.5% of medicinal plant products, and includes 31.5% of tree species (Delvaux et al., 2009). Fuel wood is the main sources of energy for domestic and processing use throughout the Sudanian and Zambezian Regions (Chidumayo, 1997; Daïnou et al., 2008; Syampungani et al., 2009; Chirwa et al., 2014). Cash crops in Mozambique, Malawi and Tanzania, include flue-cured tobacco, groundnuts, maize and cotton (Timberlake and Chidumayo, 2011), while in most of Sudanian countries, land clearing for the cotton fields is widespread (CENAGREF, 2016). In the Sudanian Region of West Africa, in general, NTFPs make up 39% of the annual income and the major contributors are woodland tree species (Vodouhê et al., 2009, 2011).

3.5.2. Main drivers of woodland change

The most drastic and directly obvious land use change is the conversion of woodlands to arable land and settlements. Especially in the Sudanian and Zambezian Regions, land use change was strongly accelerated during the last 30 years (Malambo and Syampungani, 2008; Brink and Eva, 2009) and different drivers were pointed out. Studies showed that slash-and-burn agriculture, harvesting of construction poles and fuel wood (including charcoal production) are by far the main drivers of vegetation change, both in terms of structure and floristic composition (Kalaba et al., 2013). In all sub-Saharan Africa, cultivated land increased by ca. 60% within the 1975–2000 period at the expense of natural vegetation (Brink and Eva, 2009). In the Miombo woodland, the land conversion ranged from 2 to 22% per annum due to slash and burn agriculture and charcoal production (Malambo and Syampungani, 2008). Traditional management strategies are increasingly being replaced by a dynamic, market-oriented agriculture dominated by cash crops like cotton, tobacco and cashew (Augusseau et al., 2006; Assédé, 2014; Chirwa et al., 2014). Actually, it resulted in great woodland cover loss and sometimes deforestation (Syampungani et al., 2009). The relation between human population growth and woodland change is easy to understand. The boom of human population, coupled with the drive to monocultures, has led to higher demand for firewood, charcoal and timber, thus increased woodland degradation and modification (Stephenne and Lambin, 2001; Chirwa et al., 2014). Human population growth rate, for example in West Africa, is estimated to be up to 4% y^{-1} (F.A.O, 2010). Excessive industrial activities, such as mining and commercial agriculture and forestry, are also additional sources of pressure on the woodlands in the two regions.

As driver of woodland change, intensive cultivation has fragmented and converted significant portions of the Sudanian and Zambezian woodland. Induced fire and livestock grazing and browsing are also major drivers of the woodland (Zida et al., 2007). Livestock browsing and debarking were found to severely damage saplings and reduce coppice regrowth both in Sudanian and Zambezian Regions (Geldenhuys and Williams, 2006; Delvaux et al., 2009; Van Damme and Delvaux, 2012). In fact, most of woodland drivers are interlinked. Combined effects of livestock browsing, wildfire and cultivation ultimately alter soil structural integrity, the decline of microbial biomass, as well as the loss in primary production and therefore the species diversity (Van Veen and Paul, 1981; Srivastava and Singh, 1989). Cultivation of woodland lead to important change in soil nutrients (organic matter C, P and N) (Aweto, 1981; Werner, 1984; Assédé et al., 2012c) as compared to virgin woodland. It is established that soil modification through loss in soil microbial biomass impacts significantly biological activities and plant regeneration (Juan-Baeza et al., 2015; Chaturvedi and Singh, 2017; Nyirenda et al., 2019) and imperatively lead to the establishment of invasive plant species (Perrings et al., 2002). Compared to native species which are under strong competition for nutrients, the majority of invasive plant species develop high capacity (high seed density and efficient dispersal mechanisms) to adapt to severe woodland disturbance (Sharma et al., 2005; Fandohan et al., 2015).

Many of the mapping exercises that show a change away from woodland to cropping, were once-off studies. They did not consider the development stages from abandoned cropping back to semi-mature to mature woodland. Vast areas in the Zambezian region show the increasing density of former more open woodland becoming very diverse, and productive recovering woodland, as shown by Geldenhuys (1977, 2014), Syampungani et al. (2010, 2016), Geldenhuys et al. (2013, 2017), Assédé et al. (2018), Nyirenda et al. (2019), Chichinye et al. (2019). All this fast regrowth contributes to recovery of plant diversity, and faster current sequestration of carbon in the young fast-growing stands at high density (Syampungani et al., 2010; Geldenhuys et al., 2017; Chichinye et al., 2019). So what happened over millennia with natural environmental changes, as described in this review, is probably still continuing in many areas. And resource use can be managed sustainably in the context of the varied adaptations of the tree species to survive varied disturbances and changes in these systems. Even with the increasing human population, part of this woodland dynamics can be maintained when implementing sustainable resource use in line with the natural vegetation dynamic systems, maintaining the cyclic recovery via coppice regrowth from rootstocks, fast growth of regeneration, nutrient cycling, with maintaining diverse resource use. Yes, there is loss in some areas, but there is also gain of the benefits in many other areas – all contributing to diverse woodlands, and to a large extent maintaining the ecological processes.

The sustainable management of woodland use is far from simple because the ability of trees to recover after harvesting is species-specific and depend on the inflicted wound (Delvaux et al., 2009) and sprouting vigor of harvested trees (Syampungani et al., 2016; Chichinye et al., 2019).

4. Conclusions

The comparative analysis of Sudanian and Zambezian woodlands showed great similarities and differences. The main drivers of change are quite similar. Both biogeography (continental break-up) and land use change explain the vegetation differences between the Sudanian and Zambezian regions. The absence of single-species dominant vegetation in the Sudanian region is derived mainly from the relative absence of tectonic activities. The existing traditional land use systems can be adapted to promote sustainable development at rural household level. Large-scale commercial agricultural cropping systems need to be scaled down to more realistic, integrated, multiple-use management systems. It is crucial to maintain the balance between human uses of the woodland and the capacity of the ecosystem components to recover from human induced change and stress. This will provide the incentive for both humans and woodlands to support each other. Even if biodiversity conservation goals cannot be realistically established and achieved without consideration of human livelihoods and well-being, land use planning is important to provide for the diverse, multiple and integrated use needs.

Author contributions

ESPA, CJG and PWC, conceived the ideas; ESPA conducted the literature review and led the writing process with assistance from CJG and PWC and BSSH; FAA produced the maps with assistance from ESPA, CJG and BSSH. Anonymous reviewers provided insightful comments to improve the quality of the manuscript.

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