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**Research Article**

# Impact of shifting cultivation on dense tropical woodlands in southeast Angola

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Abstract
Dry tropical woodlands are the characteristic natural vegetation type of southeast Angola, where precipitation is seasonal and nutrient content of soils is very low. Subsistence farmers overcome the poor abiotic conditions by using shifting cultivation based on specific site selection. We describe the vegetation composition of a previously unstudied dense woodland tract, which is preferred for agriculture, comparing it to nearby open woodland. We placed 25 vegetation plots randomly in the two types of natural woodland vegetation (open and dense) as well as in fallows with three different durations of land use. In each plot the cover of all vascular plant species was recorded. Variables describing vegetation structure, including basal area and leaf area index, were recorded. We analyzed soil samples for texture, pH, conductivity and nutrients, and investigated the impact of land use duration on woodland regeneration. We found that species composition and vegetation structure of the dense woodland differed greatly from the surrounding open woodland. The dense woodland is preferable for agriculture because of its higher soil content of silt, clay and potassium, higher woody biomass, and more abundant soft litter. A longer duration of land use affects species composition and diversity of the regenerating vegetation as well as nutrient content in the soil. In the near future, the increasing demand for agricultural land is likely to change the structure and composition of the dense woodland.

Keywords: dry forests, fire, Kalahari, Okavango, slash and burn agriculture, succession

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## Introduction

Shifting cultivation involves the clearing of vegetation, usually by slashing and burning, and a few years of cropping, followed by a fallow period in which farmers shift to surrounding areas [1]. In the past, the majority of studies focused on the ecological impact of slash and burn agriculture in the tropical rain forest and more studies from dry tropical forests are needed [2]. Dry tropical forests cover more than 60 % of sub-Saharan Africa and are home to a disproportionate number of people below the poverty line, many of whom depend on the woodlands for their livelihoods [3]. The area required for agriculture in this region is increasing due to population growth. At the same time, the Miombo woodlands of southern Africa have been identified as a tipping point for the Earth system. Reaching such a tipping point would lead to significant changes in biodiversity and provision of ecosystem services [4]. Therefore, investigations of the impact and sustainability of shifting cultivation by a growing population are increasingly important.

Southeast Angola is part of the larger Zambezian dry deciduous forests identified by White [5]. However, descriptions of the vegetation of the area are restricted to broad vegetation units [6, 7]. A first classification of the woodlands along the Cubango River by Revermann and Finckh [8] identified dense *Baikiaea-Burkea* woodlands, the preferred locations for shifting cultivation. These woodlands are distinguished from the otherwise dominant open woodlands of the surrounding area by their closed canopy, thicket-like understorey, and unique species composition.

Conditions in southeast Angola are unfavorable for agriculture, with highly variable rainfall [9] and predominantly sandy soils that have low water and nutrient retention capacity [10, 11]. The subsistence farmers in southeast Angola, with limited knowledge of modern soil conservation techniques and little or no access to chemical fertilizers, overcome the low productivity of the ecosystem by using shifting cultivation. New fields are created by cutting the shrubs and trees down and burning the vegetation afterwards. The burning process has a fertilizing effect on the soil through the ash, but also causes a substantial loss of nutrients through volatilization [12]. An adequate choice of the most suitable sites for cropping is paramount [1].

The ecosystem's potential to regenerate is of great importance in areas where there is long-term use of shifting cultivation. When a field is abandoned, plant regeneration and succession start. In dry tropical forests, the deforestation may initially lead to increasing grass production [13]. In general, fast-growing pioneer species with high light demand establish first and are replaced in time by increasingly shade-tolerant species [14]. This succession process is strongly influenced by soil conditions [15, 16] and the intensity and duration of former land use [17]. Longer land use can reduce biomass [18, 19], the seed bank [20] and biodiversity [16]. Biodiversity is essential to the resilience of the ecosystem as a whole [21] and so is important to conserve. Therefore, it is instructive to compare the species composition and diversity patterns in the natural vegetation to those of the fallows.

In our study area the regeneration of the vegetation is particularly important to the sustainable use and stability of the ecosystem, as shifting cultivation is concentrated in the spatially limited dense woodland. The preferred cropping sites have high agricultural productivity and are often re-used after a certain fallow period. The agricultural usage of the dense woodland patch under study has increased greatly within the last decade, and is evident from satellite data [22]. This means that the existence of this unique vegetation type might soon be threatened by expanding agricultural use. As pristine areas decrease, fallows might be reused earlier and fields might be cultivated for longer periods of time. Hence, a crucial question is whether longer usage of fields has a negative impact on regeneration processes of the vegetation and soils.

The major goals of this study are to:

(1) describe the species composition, diversity, and structure of the dense woodland and compare it to the surrounding open woodland matrix;

(2) determine whether abiotic conditions in the dense woodland differ from the open woodland, and why the dense woodland is preferred for agriculture;

(3) determine whether the duration of agricultural use has a negative impact on the regeneration, species composition, vegetation structure, and soil properties of the fallows.

## Methods

### *Study site*

The study site is in the province of Cuando Cubango in southeast Angola, 10 km west of the Cubango River. The mean annual precipitation is 732 mm, and the mean annual temperature is 22.5° C, with a mean of 17 frost days per year [9]. The region has a dry season from May to September and a growing season from November to April [9]. The soils are predominantly arenosols, consisting of a thick layer of Kalahari sands, which have been deposited by aeolian transport [10].

Literature about the vegetation of southern Angola is sparse. The main vegetation types are closely related to those of the Kavango woodlands of northern Namibia as described by Burke [23] and Strohbach & Strohbach [24]. A related vegetation type sharing many tree species is the 'chipya' vegetation of Zambia [25]. Other sources classify the study region as *Baikiaea* woodland but lack phytosociological data [26]. Recent classification of the vegetation of southeast Angola defines the region as *Baikiaea-Burkea* woodland [8]. Land use in this open woodland is restricted to timber cutting and small-scale livestock farming for local needs. Fire events play a major role in this vegetation unit [27], and many of the present plant species show signs of fire adaptation such as thick corky or peeling bark [28].

While the open *Baikiaea-Burkea* woodlands dominate the landscape of the region, the dense woodland resembles a vegetation unit with a spatially very limited extent and is clearly distinguishable from the surrounding open woodland on satellite images. The dense woodland patch under study (16°43'00''S 17°47'00''E, Fig. 1) forms the largest continuous area of this vegetation unit in the region with about 14,800 ha extending for about 20 km in a northwest–southeast direction parallel to the Cubango River. It is not mentioned in the vegetation map of the province of Cuando Cubango [7] and was first mentioned in 2013 [8]. Following an automated classification of topography, based on data from the Shuttle Radar Topography Mission [29], there is no notable difference in topographic position between the dense and open woodlands (Appendix 3).

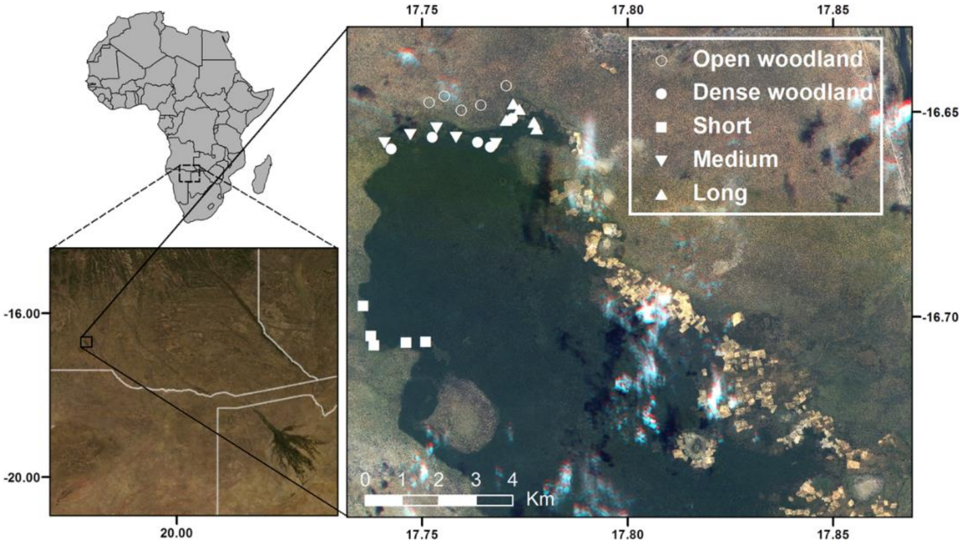

**Fig. 1. Location of the study site in southeast Angola. Source: Rapid Eye AG [33]; Acquisition date: 03/18/2013; Units: decimal degrees; Map datum: WGS84.**

The population density in the region is below 1 person km$^2$, and the villages are concentrated along the river [30]. A gravel road follows the Cubango River on its western bank, but the exchange of goods is rather low as there are no nearby cities. The Namibian border is 100 km to the south and the city of Menongue is 230 km to the north. The predominant crops in the fields are a mixed culture of maize or millet with beans and groundnuts. The soil is prepared with hoes and ox-drawn ploughs, and seeds are sowed with the beginning of the rainy season from October to November. The number of years a field is used for cropping strongly depends on how fast soil fertility declines. A typical crop duration is estimated to last two to three years.

*Data acquisition*

On the satellite images fields are recognizable as rectangular features that appear at the fringes of the dense woodland. To inform site selection we used a time series of satellite images. Based on a combination of Google Earth imagery [31], Landsat scenes [32], and RapidEye imagery [33] we visually assessed land-use history of the fields in the dense woodland (Appendix 4). The detected fields differ in the dates when they were first cultivated, but were all abandoned in 2001. Consequently, the fields that are currently fallows were subject to different durations of agricultural use. These fallows were grouped into three categories according to the duration of cultivation: short (ca. 4 y), medium (ca. 9 y) and long (ca. 14 y) periods. Because the available time series does not provide suitable images for each year, it is possible that some fields have not been used continuously during the periods in question. For field investigations, five random points were generated for each of the three disturbed vegetation types: 'short use/fallow', 'medium use/fallow', and 'long use/fallow', as well as for the two types of undisturbed vegetation: 'open woodland' and 'dense woodland' (Fig. 2). Field investigations took place in February 2013, when fallows had an age of 12 years.

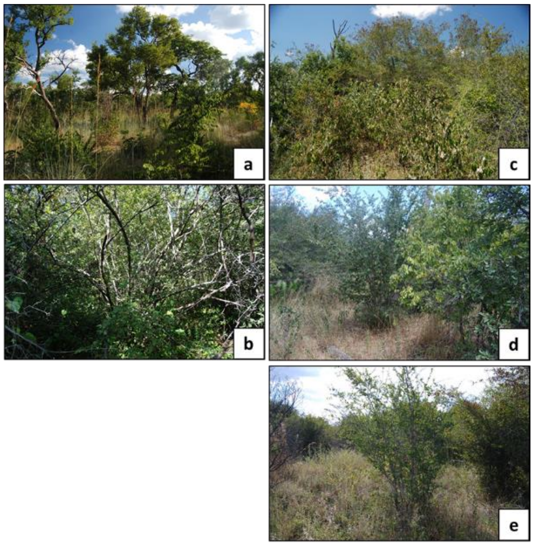

**Fig. 2. Photos of the five categories. a = open woodland (24202), b = dense woodland (24178), c = short use/fallow (24188), d = medium use/fallow (24170), e = long use/fallow (24166). Photos by J. Wallenfang**

On vegetation plots sized 20 m × 50 m, we took an inventory of all vascular plant species and estimated the vertically projected cover of all species. We followed the taxonomy of Figueiredo and Smith [34]. We collected herbarium specimens for species not identifiable in the field. Specimens were deposited at the Instituto Superior de Ciencias da Educação in Lubango (LUBA), Angola, and Herbarium Hamburgense at the Biocentre Klein Flottbek (HBG), Germany.

We measured vegetation structure by estimating total vegetation cover per plot and the percentage covered by plants in the following strata: 0-0.5 m, 0.5-2 m, 2-5 m, 5-10 m and 10-20 m. Additionally, cover values for mosses, lichens, soft litter (leaves), and hard litter (twigs, stems) were recorded. We measured the maximum height and the height of the lower 95% of the vegetation ('main height') in order to exclude single emergent trees. We estimated the duration since the last fire in the categories 1, 2, 5, 10, >10 y based on indicators such as presence of annual species, burned culms of grasses or bark of trees, and charcoal on the ground and in the soil. Signs of grazing animals such as browsed culms and traces were noted. We took hemispherical photos to determine the site-specific Leaf Area Index (LAI) at five locations (distance 12.5 m) per plot at a height of 1.3 m. The LAI was calculated after Lang [35] with the software Hemisfer [36]. The threshold was detected automatically after Nobis and Hunziker [37] and adjusted manually if the automatic detection failed. The correction for non-linearity and slope was used [36]. Because hemispherical photography cannot differentiate woody and leaf material, the LAI is more appropriately described as plant area index (PAI) [38]. As a proxy for standing woody biomass we recorded the height and the diameter at breast height (DBH) of all trees with a DBH > 5 cm. In order to capture the biomass of shrubs and small trees with DBH < 5 cm, all stems higher than 2 m were recorded in a nested subplot of size 10 m × 10 m. Based on the DBH measurements, we calculated the basal area (BA) per hectare according to equation 1. BA was calculated separately for trees with DBH > 5cm ($BA_{trees}$) and saplings and shrubs with a DBH < 5 cm ($BA_{shrubs}$).

Equation (1) $$BA = \sum(\pi \times (DBH_i/2)^2) \times 10$$

With BA = Basal area in $m^2$ per hectare; DBH = diameter at breast height in m; for trees on the 1,000 $m^2$ plot result was multiplied by 10, and for shrubs on 100 $m^2$ plot by 100, to convert BA to the value for one hectare.

A comprehensive analysis of the edaphic conditions was carried out to assess whether differences in vegetation arise from different abiotic conditions. At every plot four soil samples were taken at standardized depths: 0–10 cm, 25–45 cm, 70–90 cm, and 180–200 cm. The following physical and chemical soil properties were assessed for each sample: conductivity, pH in a 0.01 M $CaCl_2$ solution, grain size according to the USDA classification, and nutrient contents for potassium, calcium, magnesium, and sodium via a 1 M NH4–acetate–EDTA extraction, and phosphorus via a 0.001 M sulphuric acid extraction.

### *Data analysis*

We carried out an indicator species analysis using the indicspecies package in R [39, 40] to identify characteristic species of each vegetation category. For each species we calculated the *phi* value in order to test for the strength of a species' association with each category. The *phi* value ranges from -1 to 1. Positive *phi* values indicate that the species and the vegetation unit jointly occur more frequently than expected by chance [41]. To compare plant diversity of the five categories we calculated diversity profiles. Instead of calculating a few arbitrary selected diversity indices, the diversity profiles have the advantage that they allow a more complete picture of the multidimensional term diversity [42]. The scale parameter α can be mathematically converted to common diversity indices. Low α values represent diversity indices focusing on species richness, while with increasing α more weight is given to the aspect of evenness, *e.g.,* α=0 is related to species richness, while α=1 to the Shannon diversity index, and α=2 to the Simpson index [43]. When two profiles do not intersect, the profile with the higher Hα values can be considered more diverse. The diversity profiles were calculated with the vegan package [44] in R 3.0.1 [40].

We used a detrended correspondence analysis (DCA) to investigate the variation within the species composition. The DCA is known to avoid the arch effect common in multivariate vegetation data. The arch effect occurs in a standard correspondence analysis when data sets that are missing the same species data are considered more similar than data sets that share a common species pool [45]. DCA was computed in PC-Ord 5 with 26 segments, rescaled axes, and down-weighted rare species. We also computed a Principal Component Analysis (PCA) on the matrix of environmental variables to identify the abiotic conditions prevailing in the four categories [45]. PCA uses the linear distance measure Euclidean Distance, which is suitable for environmental data. We applied Kruskal-Wallis, Mann-Whitney and *t*-tests in PAST 2.16 [46] to test for significant differences in structural and soil variables among the categories.

## Results

### *Floristic composition*

A total of 187 species were found within the 25 vegetation plots. 76% of the species were identified to species level, 9% to genus level and 15% remained unidentified. As Figure 3 clearly shows, the five land cover classes / vegetation strata clearly differ in their vegetation composition, with the exception of the young and medium fallows, which were broadly compositionally similar. In the open woodland plots tall trees like Ordeal tree (*Erythrophleum africanum*) and Large false mopane (*Guibourtia coleosperma*) have a high *phi* value and are frequent (Appendix 5). The shrub layer is characterized by tall shrubs such as Horn-pod tree (*Diplorhynchus condylocarpon*), Peeling plane (*Ochna pulchra*) and Bicoloured bushwillow (*Combretum collinum*). The herb layer is defined by different grasses of the genera *Trachypogon*, *Hyparrhenia*, *Eragrostis*, *Aristida* and *Digitaria,* and sedges of the *Cyperaceae* family. Some herbs such as *Tephrosia lupinifolia* and the small shrub *Dichapetalum rhodesicum* are characteristic of the open woodland. In contrast, the dense woodland is a mixture of tall-growing (ca. 6 m), multi-stemmed shrub species like Satin-bark corkwood (*Commiphora tenuipetiolata*) and Jesse-bush bushwillow (*Combretum celastroides*) and tall (ca. 11 m) single-stemmed species, mainly Zambezi teak (*Baikiaea plurijuga*) and single individuals of Kalahari apple-leaf (*Philenoptera nelsii*). In the understorey several herbs occur, *e.g.,* Creeping foxglove (*Asystasia gangetica*), *Alectra picta*, *Ocimum* sp. and *Hibiscus* cf. *mastersianus* as well as lianas of the Apocynaceae family and *Ipomoea dichroa*. The small spiny tree species Flame thorn (*Acacia ataxacantha*) and Sicklebush (*Dichrostachys cinerea*) are characteristic and frequent in short and medium use/fallows. A few herbs are indicative of certain fallow types, such as *Hermannia eenii* which mainly occurs on short use/fallows, *Justicia bracteata* on medium use/fallows and Gemsbok cucumber (*Acanthosicyos naudinianus*) on long use/fallows. In the dense woodland, grasses are nearly absent, but grass species of the genera *Panicum*, *Digitaria* and *Urochloa* are characteristic of short use, long use and the combination of short and medium use/fallows respectively. *Eragrostis cylindriflora s.lat.* is characteristic of the combination of all three fallow types.

Detrended Correspondence Analysis (DCA) visualizes the differences in the species composition among the vegetation plots (Fig. 3). The length of the first axis (standard deviation, SD = 5.68) is larger than a single complete turnover in species composition (*i.e.,* > 4 SD) [47] and illustrates a strong separation of the open from the dense woodland. The three fallow categories cluster near their original state (*i.e.,* dense woodland) in the first axis. The second axis (SD = 2.46) mainly displays the difference in species composition between the dense woodland and the long use/fallows, whereas the medium and short use/fallows are not separated. The distances between plots within each of the undisturbed categories (*i.e.,* dense and open woodland) are less than within the fallow categories, indicating more homogeneity of the undisturbed woodlands.

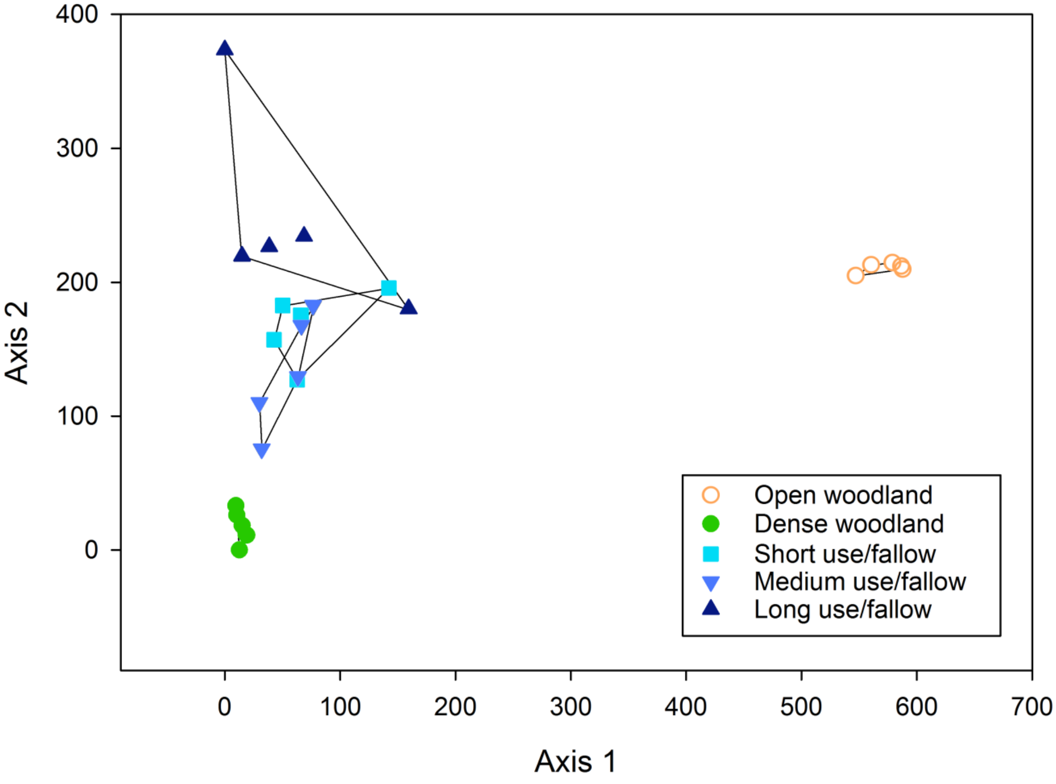

**Fig. 3. Detrended Correspondence Analysis showing groups of vegetation plots, marked by convex hulls. Ordination diagram with axis 1 and 2 (standard deviation*100); convex hulls were drawn post-hoc.**

In general, species diversity is relatively high (Fig. 4), with Shannon diversity (α = 1) ranging from 2.5 in the dense woodland to 2.9 for long use/fallows, 3.0 for medium use/fallows and open woodland, to 3.2 for the short use/fallows. Diversity profiles show that the categories in general are similar for low α-values and diverge with increasing α. Differences are not significant for species richness (Kruskal Wallis: H = 3.2, df = 4, P = 0.528) but increase if abundances of species are taken into account. The Hα-values are consistently lower in the dense woodland than in the other categories. Short use/fallows have a higher diversity than the other fallow categories and the open woodland, except for species richness. The remaining line comparisons intersect.

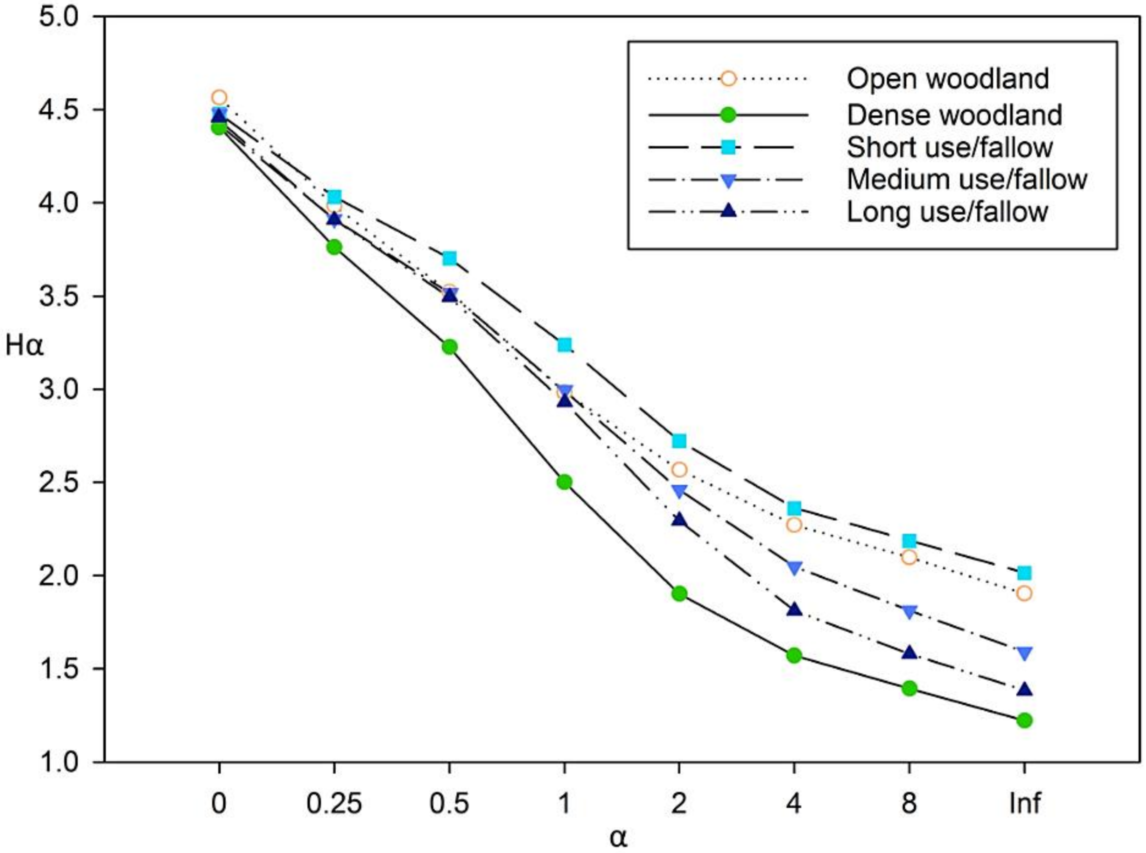

**Fig. 4. Diversity profiles of five vegetation plot categories using Renyi's diversity (Hα). The scale parameter (α) gives the order of Renyi's diversity; α = 0 is the logarithm of species richness, α = 1 equals the Shannon diversity index, α = 2 is the logarithm of the reciprocal Simpson diversity index, α = Inf refers to the proportion of the most abundant species.**

*Vegetation structure and soil conditions*

The first axis of the PCA (Fig. 5) explains 17.2% of the total variance and separates the dense woodland from the other categories. Although this value seems low, it can be explained by the large amount of parameters (=84) that entered the PCA. The LAI, the cover of the shrub stratum 2–5 m, soil sand content, and the soil pH explain the variation in the first axis. The open woodland is clearly separated from the other categories along the second axis, explaining 14.8% of the total variance. This axis is characterized by a strong grazing gradient, fewer nutrients and lower values for total vegetation cover and herb cover. The three fallow categories cannot be clearly separated via the PCA. Generally, the variation within a category is lower for the undisturbed habitats compared to the fallow categories. For correlations of all variables with the first three axes of the PCA and full names of variables, see Appendix 6.

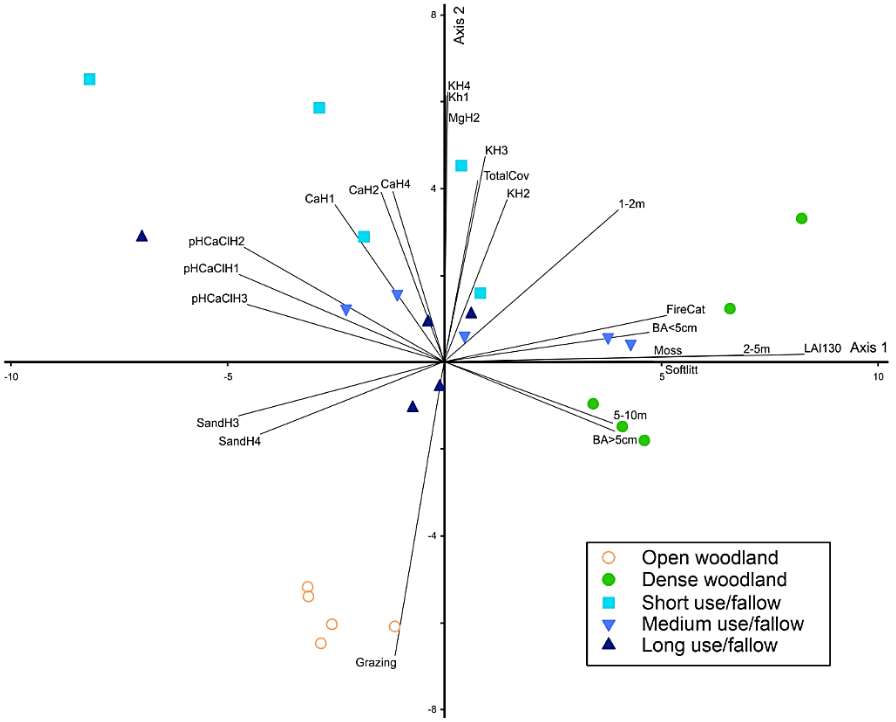

**Fig. 5. Principal Component Analysis of structural and soil variables. Scores calculated by weighted averages (Euclidean distance); only variables with an $R^2 > 0.4$ for the joint plot are shown; for details of variables see Appendix 6.**

The open woodland is characterized by lower total cover values (ca. 60%, Appendix 1), lower cover values in all strata, and a low LAI (0.8). The basal area for trees and the main height is relatively tall (9.5 m). The open woodland exhibits grazing and frequent fire events; mosses and lichens are not present. The soils are sandier in the open woodland compared to the other categories (Appendix 2). In general, the soils are nutrient- poor.

The dense woodland is characterized by close vegetation, with the 2–10 m cover and total cover values reaching 97%, the highest of all sites; LAI are also relatively high with a mean of 2.8. The dense woodland exhibits a high BA for the shrubs, the highest BA value for trees and the tallest trees. Furthermore, the dense woodland reaches the highest values for soft litter, moss and lichen cover (Appendix 1). Additionally, no fire enters the dense woodland (high value for FireCat). For its soil properties, clay ($t = 5.05$, $df = 19$, $P < 0.001$) and silt ($t = 2.32$, $df = 19$, $P < 0.05$) contents are significantly higher than in the open woodland.

The fallows have a relatively high total vegetation cover (79%–87%) due to their dense shrub layer (Appendix 1). The basal area in the fallows is low with high variablity. The LAI in the fallows ranges from 1.2 to 1.6 with a high standard deviation (0.5–0.9). Nutrient contents for potassium ($K^+$), calcium ($Ca^{2+}$) and magnesium ($Mg^{2+}$) are higher in some fallows (Fig. 5). Tests on differences show that $Ca^{2+}$ is significantly higher for short use/fallows than in the other groups (Mann-Whitney: $U = 2$, $n = 5$, $P < 0.05$), but there are no significant differences among the other groups. The $Mg^{2+}$ content is significantly higher for short use/fallows than for the open woodland (t-test for equal variance: t = 6.27, df = 4, $P < 0.01$) (Appendix 2).

Significant differences were found for potassium among the categories (Kruskal-Wallis: H = 54.6, df = 4, $P = 3.5 \cdot e^{-11}$) except for the dense woodland and medium use/fallows (Fig. 6). The open woodland (56–111 mg $kg^{-1}$) has a lower concentration of potassium than the dense woodland (250–325 mg $kg^{-1}$). The potassium values for the fallows show a gradient from short use/fallows to long use/fallows. Compared to the dense woodland, the short use/fallows have higher potassium values (360–570 mg $kg^{-1}$), the medium use/fallows are at the same level (196–243 mg $kg^{-1}$) and the long use/fallows have lower values (134–159 mg $kg^{-1}$, Fig. 6).

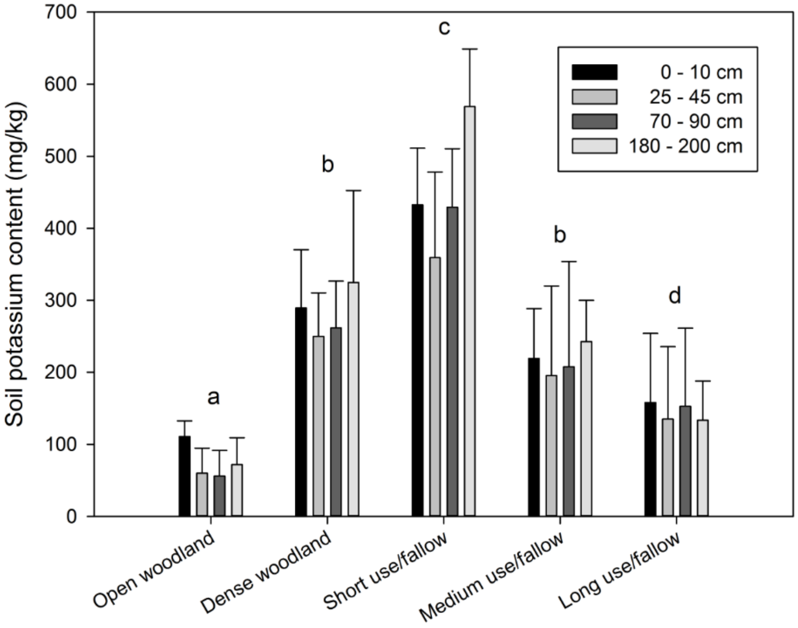

**Fig. 6. Soil potassium content of the vegetation categories for different soil depths. Whiskers display standard deviation; letters indicate significant differences between categories with $p < 0.05$ according to Mann-Whitney pairwise comparisons.**

## Discussion

### *Species composition, structure and diversity of the dense woodland*

**Woodland species composition and structure**

The analysis of the species composition shows an almost complete species turnover from open to dense woodland. This is especially interesting, as there was no apparent environmental gradient or notable ecotone separating the two woodland types.

The open woodland is similar in species composition to the Kavango woodlands of northern Namibia [23, 24], where nutrient-poor soils, seasonally dry conditions and frequent fires are the main ecological drivers [23, 48]. Many species show adaptations to fire, such as woody species with thick corky or peeling bark, or perennial grasses forming dense tufts, which protect the buds and allow for resprouting after fires. In contrast, in the dense woodland the upper canopy is formed almost exclusively by Zambezi teak (*Baikiaea plurijuga*) which has a rather thin bark and is regarded as fire sensitive [49]. Kalahari apple-leaf (*Philenoptera nelsii*) is the second tree species reaching the lower canopy.

Furthermore, the dense woodland supports a dense shrub layer formed by species such as Satin-bark corkwood (*Commiphora tenuipetiolata*), Lavender croton (*Croton gratissimus*), and Jesse-bush bushwillow (*Combretum celastroides*). The closed canopy creates a self-sustaining, cooler and more humid micro-climate, with shady conditions for specialized herbs, climbers, and large quantities of mosses and liquens. These microclimatic conditions conserve moisture, favour plant growth, and hinder ground fires. The absence of high grass coverage also impedes the spread of ground fires [50]. Our field observation that wild fires never entered the dense woodland in the recent past is also supported by Frantz *et al.* [51], recording no fire in the dense woodland within the years 2001-2012, based on the MODIS burned area product.

### Woodland species diversity

Plant species diversity in the open woodland was higher in both species richness and evenness aspects than in the dense woodland, probably due to frequent disturbance by fire and grazing (Fig. 4). The dense woodland can be regarded as undisturbed by large herbivores, allowing a clear and homogenous vegetation structure to develop. A few species dominate, resulting in a lower evenness than in the open woodland. In contrast, the species richness does not differ between the woodland types with mean values of 48.6 species per 1000 $m^2$ for the dense woodland and 50.2 for the open woodland. These values are slightly higher than those cited for plots of equal size in the Kavango woodlands of northern Namibia, with 43.8 species for the observatory Mile 46 and 42.5 for Mutompo [52].

### Differences in environmental factors among open and dense woodland

What are the environmental factors facilitating the occurrence of dense woodlands? Because our results are not conclusive with regard to this question, we can only speculate about the determining environmental factors. However, we can report some salient features: the sharp transition from open to dense woodland, the changes in vegetation taking place within a few metres; the lack of notable differences in elevation or topographic position; and a notable change in soil texture, which indicates geogenic differences in soil conditions. Furthermore, there are clear differences in grazing and browsing regime and in the frequency of fire events. In contrast to the open woodland, grazing as well as fire are literally absent from the dense woodland. Both factors have been shown to be major determinants of vegetation patterns in Southern Africa [53, 54]. However, in this case we consider them not as the primary drivers, but as factors sustaining the current state of the distribution of the two coexisting vegetation units, as discussed below.

The dense woodland has a significantly higher silt (6.4 %) and clay (4.9 %) content than the open woodland (2.8 % and 1.0 % respectively), thus providing a higher moisture retention capacity. This is an important factor as rainfall is seasonal [9] and water for vegetative growth needs to be stored. Furthermore, the higher content of potassium in the dense woodland soils offers better growing conditions. This level of potassium can be explained in two ways. Firstly, the higher clay content enhances cation exchange capacity and thus favors nutrient retention. Secondly, the lack of fire events in the dense woodland means that plant material is not volatilized but instead decomposed.

In contrast, low potassium contents in the open woodland can be explained by losses through volatilization, ash convection, and erosion, as well as leaching after frequent burning processes [12, 55]. The content of organic carbon in the soil, although it was not measured, is expected to be higher in the dense woodland due to being undisturbed by fire. A higher content of soil organic carbon might also increase moisture retention capacity and nutrient retention. The macro nutrient nitrogen was not measured, and for phosphorus no trend was found and the values showed a high standard deviation (Appendix 2). Although the differences in soil properties between open and dense woodland are small, these differences are important in a very nutrient-poor environment.

### Similar vegetation types from the Zambezian phytoregion

A similar type of 'cryptic' dense woodland is known from northern Zambia: the Itigi-Sumbu thickets. They have a very similar structure, have sharp borders with the surrounding vegetation, and feature very shady, moist conditions [5]. They even share the species Jesse-bush bushwillow (*Combretum celastroides*) with the dense woodland in our study. An additional similarity is the preference for agriculture in these patches. Although this is a different ecosystem, with higher precipitation and surrounded by Miombo forests, the underlying biophysical conditions may be similar. White [5] links the occurrence of those Itigi-Sumbu thickets to an impermeable duricrust beneath a sandy soil of 0.6–3 m. In our case such an impermeable underlying structure would restrain infiltration and facilitate accessible groundwater reservoirs. It has been shown that available soil volumes over calcrete crusts, in combination with rooting depth, determine vegetation composition in the Kavango region of northern Namibia [48]. Sicklebush (*Dichrostachys cinerea*), a species we found in the dense woodland and fallows, is mentioned by Burke [23] as a species profiting from hard subsoil structures and shallow soils. However, we did not find a hard crust within the two metres of soil depth analyzed.

Dense vegetation patches or thickets occur occasionally in the whole Zambezian phytoregion [5]. They are often related to secondary vegetation created by human activity (*e.g.,* livestock farming). However, both the Itigi-Sumbu thickets and the dense woodland of this study represent seemingly undisturbed vegetation. A contrasting hypothesis for the origin of the dense woodland would be a relict ecosystem resulting from the transformation of the surrounding landscape. However, such a change in environmental conditions would have to occur on a very long time scale, as the shape and boundaries of the dense woodland on satellite images have been constant since the oldest available Landsat images in 1972 (Path: 178, Row: 072).

### Benefits of the dense woodland for agriculture

Several factors make the dense woodland more attractive for agriculture than the open woodland. As discussed above, soils in the dense woodland offer slightly better growing conditions. Furthermore, the basal area – which is an approximation for standing woody biomass – is higher in the dense woodland. In the basal area of shrubs, we found a more than tenfold increase, from 0.4 $m^2$ $ha^{-1}$ in the open woodland to 4.7 $m^2$ in the dense woodland. The shrubs burn easily and add ash and nutrients to the soil, in contrast to trees with larger stems, which are not easily burned. Furthermore, the LAI is almost three times higher in the dense woodland. The larger amounts of leaves and accumulated soft litter mean that more nutrients are released during the slash and burn process and fertilize the soil [12].

Farming in dense woodland sites promises better yields than in the surrounding open woodland. The described advantages apparently outweigh the additional effort in terms of labor and also access: the sites are a distance of about 8–10 km from the river, village and road. To compensate, during the cropping season people move their homes to the hinterland and organize daily water supplies via oxcart.

### *Impact of duration of agricultural use on regeneration*

### **Diversity of fallows**

Compared to the woodlands, the regenerating fallows are more heterogeneous in species composition, vegetation structure, and soil composition, and therefore have a higher species diversity than the undisturbed state.

In our study, species diversity responded to land use duration, especially for more evenness-based indices (*i.e.,* $\alpha > 1$, see Fig. 4). All fallows had a higher diversity than the dense woodland. Short use/fallows showed higher diversity than medium and long use/fallows. This pattern is in line with the predictions of the intermediate disturbance hypothesis (IDH). However, the generality of the IDH is still debated, as studies from dry tropical woodlands show [56] and do not show support for the IDH [57]. Positive effects of shifting cultivation on diversity at a landscape scale were found in semi-deciduous forests in Ivory Coast [58], dry floodplain woodlands in Kenya [59], and in Miombo woodlands of Tanzania [60]. The remaining diversity profiles intersect and hence are 'non-comparable' [42] or 'non-separable' [61].

### **Species composition of fallows**

In contrast to Luoga *et al.* [62] we found no evidence of resprouting trees from trunks above ground, therefore regeneration has to originate from seed banks, rhizomes, or dispersal from plants surrounding the fallow. This promotes fast-growing grasses and herbs, which are usually the first colonizers [13, 14]. Sicklebush (*Dichrostachys cinerea*) and Flame thorn (*Acacia ataxacantha*) are spiny plants, an adaptation to herbivory that might hamper grazing on the fallows. As the species composition of all fallows is much closer to the dense than to the open woodland, a return to dense woodland in the long term is likely. However, to verify a successional pathway to dense woodland vegetation, additional data on later stages are needed.

This regeneration pathway may actually never be realized, as economic development and population growth increase demand for agricultural land [63]. Recent work has shown substantial forest cover losses related to agricultural expansion in Angola over the last decade [22, 64]. Based on the time series of satellite images (Appendix 4) we could show that the cultivation in the dense woodland started in 1986 and was more or less static at 3% from 1986 to 2000. Since then it has increased exponentially, with 17% under cultivation or in recent fallow stages in 2013. Consequently, field fallow cycles will likely shorten, meaning the area of the dense woodland could shrink rapidly in the near future.

Our data indicate that land use duration affects fallow regeneration of dense woodlands. Long use/fallows differ more strongly in species composition from intact woodlands than fallows with shorter land use duration (Fig. 3). The species composition of the medium and short use/fallows is closer to the original vegetation. Consequently, vegetation community regeneration in the long use/fallows will take longer, which may be due to a reduced seed pool [65, 20]. Mwampamba and Schwartz [66] show for tropical woodlands in Tanzania that regeneration is impeded by long cultivation durations exceeding 16 years. For shorter time spans, as in our case, they did not find a straightforward relationship among diversity, basal area, and stand complexity. Similarly, studies from Ivory Coast [67], Madagascar [68] and South America [65] found slower species regeneration in tropical forests due to more intense and/or prolonged land use. However, a comparison of studies from different tropical regions is difficult because of site-specific differences in regeneration time, type of land use, biotic and abiotic conditions, and the different units used for measuring diversity and regeneration. For example, land use history for most study sites is vague because exact information about past land use is often not available [69].

### Structure and soil properties of fallows

In vegetation structure and soil composition, the fallows did not differ much, according to the PCA. A negative effect of land use duration on the regeneration of basal area, stem density, and biomass, as shown in other tropical regions [65, 66, 68, 16], could not be found, but a closer look at each variable revealed differences in the case of potassium. The slash and burn process volatilizes nutrients. Most nitrogen and a large share of phosphorus are lost. However, some nutrients, especially potassium ($K^+$), are conserved in the ash and act as a fertilizing pulse [12]. Our results show that after a short period of land use and twelve years of fallow regeneration, this fertilizing effect is still detectable for $K^+$ but not for phosphorus. Interestingly, with longer land use the $K^+$ content decreases and eventually reaches values below the original state (Fig. 6). Therefore, a longer cultivation period has a negative effect on the $K^+$ content, probably due to potassium export with crops. $K^+$ was shown to be a crucial factor for maize cropping in other tropical regions [70, 71]. This could be the reason why fields can only be cultivated for short time spans before yield reduction makes cultivation unattractive.

## Implications for conservation

We have shown that the dense woodland strongly differs in species composition from the prevailing open woodland. In contrast to the open woodland, the dense woodland is protected against fire events. However, it is targeted for agriculture, as its soils are slightly more fertile and the higher woody biomass produces a higher nutrient pulse when burned for shifting cultivation. The usage of the dense woodland for agriculture has increased exponentially since the year 2000. Consequently it can be expected that a new emerging cultural landscape will be created. Such a landscape, with a mixture of fields and fallows, would create a higher plant diversity [72, 60]. However, specialized species closely associated with the dense woodland may become less abundant. Furthermore, increasing demand for arable land, as described for the adjacent region [73], may lead to prolonged use of agricultural fields, influencing species composition and diversity in the regenerating fallows as well as negatively impacting soil fertility. Eventually, increased agricultural usage may lead to substantial loss of soil fertility, and consequently cropping conditions in the former dense woodland will no longer be superior to those in the open woodland.

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**Appendix 1.** Variables on vegetation structure for each category showing the average (AVG) and standard deviation (SD). Cover according to vegetation strata; main height is the maximum height of the lowest 95 % of the vegetation; basal area shrubs = sum of BA of all stems with DBH < 5 cm, basal area trees = sum of BA of all stems with DBH > 5 cm; species richness given for all vascular plants and for trees with a DBH > 5 cm.

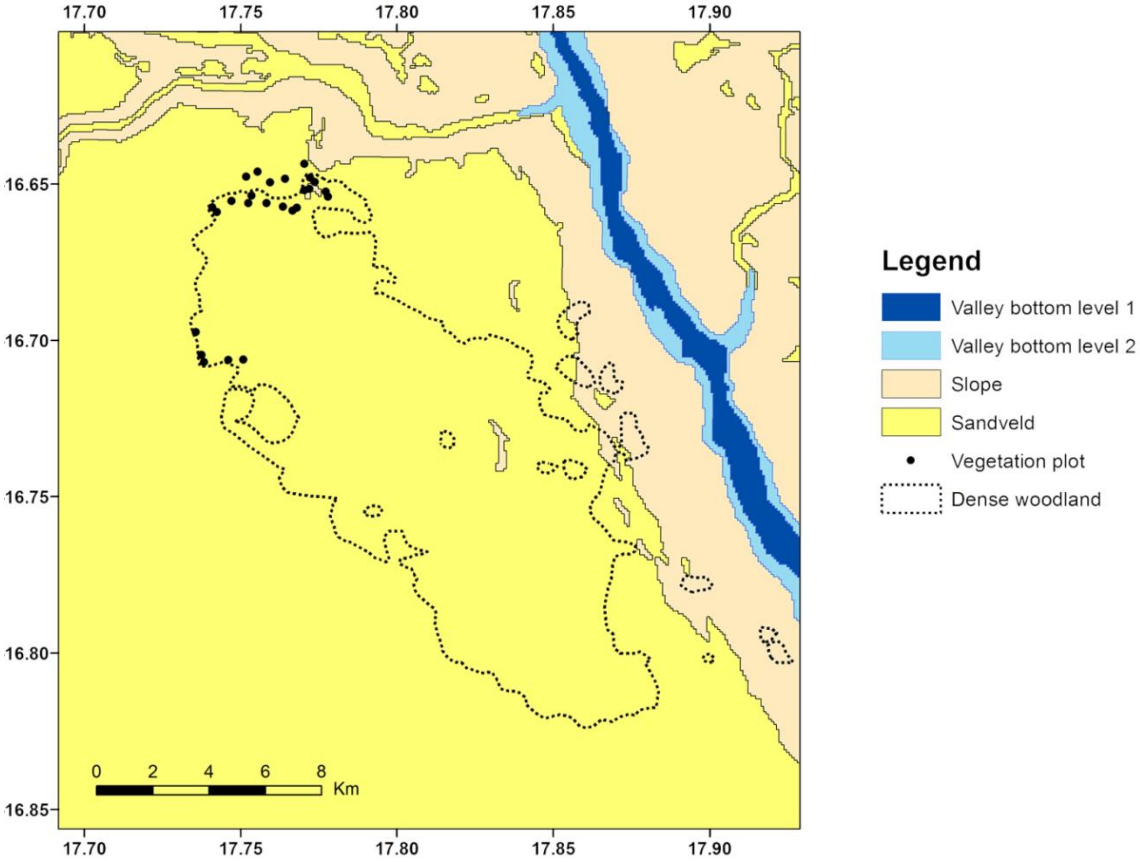
| | Open woodland | | Dense woodland | | Short use/fallow | | Medium use/fallow | | Long use/fallow | |
|---|---|---|---|---|---|---|---|---|---|---|
| | AVG | SD | AVG | SD | AVG | SD | AVG | SD | AVG | SD |
| Total Cover (%) | 61.0 | 11.4 | 96.6 | 2.3 | 87.0 | 2.7 | 79.0 | 10.8 | 86.6 | 7.6 |
| 0.0-0.5 m Cover (%) | 41.0 | 9.6 | 43.0 | 6.7 | 67.0 | 24.9 | 47.2 | 14.5 | 68.0 | 22.5 |
| 1-2 m Cover (%) | 21.6 | 9.1 | 64.0 | 13.4 | 62.0 | 13.0 | 48.0 | 13.5 | 43.0 | 18.6 |
| 2-5 m Cover (%) | 18.0 | 9.1 | 73.0 | 8.4 | 35.4 | 23.8 | 51.0 | 7.4 | 32.2 | 19.1 |
| 5-10 m Cover (%) | 15.2 | 7.6 | 28.0 | 10.4 | 4.0 | 6.2 | 10.6 | 4.4 | 10.2 | 5.7 |
| 10-20 m Cover (%) | 5.8 | 6.4 | 10.8 | 5.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 0.9 |
| Main Height (m) | 9.5 | 3.2 | 11.7 | 1.1 | 4.6 | 0.5 | 5.5 | 0.4 | 4.4 | 2.7 |
| Leaf Area Index | 0.8 | 0.2 | 2.8 | 0.4 | 1.3 | 0.9 | 1.6 | 0.5 | 1.2 | 0.8 |
| Soft litter Cover (%) | 23.0 | 26.8 | 82.0 | 11.0 | 29.0 | 20.1 | 12.6 | 7.0 | 12.0 | 9.0 |
| Mosses Cover (%) | 0.0 | 0.0 | 1.4 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Lichens Cover (%) | 0.0 | 0.0 | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Basal Area shrubs ($m^2$/ha) | 0.42 | 0.15 | 4.69 | 1.65 | 2.41 | 1.63 | 3.32 | 1.67 | 2.12 | 2.37 |
| Basal Area trees ($m^2$/ha) | 7.50 | 3.11 | 12.42 | 2.57 | 2.22 | 1.20 | 3.63 | 1.33 | 2.66 | 2.14 |
| Species richness | 50.2 | 3.8 | 48.6 | 2.9 | 50.6 | 4.1 | 50.4 | 5.5 | 46.0 | 5.8 |
| Species richness (>5 cm DBH) | 9.2 | 2.2 | 7.4 | 2.4 | 5.2 | 1.6 | 6.2 | 0.4 | 4.4 | 2.1 |
| Grazing signs | Y | | N | | N | | N | | N | |
| Fire signs | Y | | N | | N | | N | | N | |

**Appendix 2.** Average (AVG) and standard deviation (SD) values for the soil variables of the four soil depths and the five soil profiles for each category.

| | Open woodland | | Dense woodland | | Short use/fallow | | Medium use/fallow | | Long use/fallow | |
|---|---|---|---|---|---|---|---|---|---|---|
| | AVG | SD | AVG | SD | AVG | SD | AVG | SD | AVG | SD |
| $CaCO_3$ content (g $kg^{-1}$) | 0.5 | 0.6 | 0.7 | 0.9 | 0.8 | 0.5 | 0.4 | 0.4 | 1.0 | 0.6 |
| Clay content (%) | 1.0 | 1.2 | 4.9 | 2.3 | 1.9 | 1.2 | 6.9 | 1.5 | 5.7 | 1.6 |
| Silt content (%) | 2.8 | 1.0 | 6.4 | 4.6 | 3.2 | 0.8 | 4.9 | 1.3 | 4.3 | 1.1 |
| Sand content (%) | 96.2 | 2.1 | 88.8 | 5.5 | 94.9 | 1.1 | 88.1 | 1.2 | 89.9 | 2.7 |
| pH ($CaCl_2$) | 4.4 | 0.1 | 4.3 | 0.1 | 4.7 | 0.5 | 4.8 | 0.5 | 4.8 | 0.6 |
| Conductivity (µs $cm^{-1}$) | 7.3 | 1.8 | 17.0 | 9.0 | 13.2 | 1.7 | 15.0 | 2.5 | 15.0 | 2.7 |
| Potassium (mg $kg^{-1}$) | 74.7 | 25.1 | 281.5 | 76.2 | 447.6 | 61.1 | 216.3 | 93.5 | 145.1 | 56.4 |
| Sodium (mg $kg^{-1}$) | 22.3 | 2.6 | 28.1 | 11.0 | 35.0 | 6.6 | 30.3 | 15.0 | 20.5 | 1.8 |
| Calcium (mg $kg^{-1}$) | 70.1 | 14.4 | 105.8 | 58.3 | 416.8 | 174.4 | 160.9 | 79.7 | 133.7 | 123.0 |
| Magnesium (mg $kg^{-1}$) | 0.89 | 0.32 | 1.53 | 0.79 | 2.09 | 0.29 | 1.58 | 0.62 | 1.37 | 0.62 |
| Phosphorus (mg $kg^{-1}$) | 0.32 | 0.09 | 0.29 | 0.21 | 0.46 | 0.43 | 0.31 | 0.15 | 0.19 | 0.12 |

**APPENDIX 3.** Geomorphological landscape units derived from the global digital elevation model SRTM (Shuttle Radar Topography Mission, USGS 2004) following the automated classification of topography developed by Iwahashi & Pike [29]. Classification was done by Jan Wehberg; Grid cell of 90 m; Units: decimal degrees; Map datum: WGS84.

'Valley bottom level 1' denotes the current river bed of the Cubango River, 'Valley bottom level 2' the floodplain, 'Slope' the area showing a gentle slope towards the stream network, and 'Sandveld' the sandy plain of the hinterland with only very subtle differences in terrain.



**APPENDIX 4.** Calculation of fallow age and field duration with a satellite image time series. Source of Imagery given for Landsat, Google Earth and Rapid Eye; categories: S = short use/fallow, M = medium use/fallow, L = long use/fallow; values for land use intensity: 0 = not used, 0.5 = partly used, 1 = used, E = stripes on the picture (error in Landsat sensor), C = clouds.

| Plot | Category | Fallow ID | 1984 LT51780721984166AAA03 | 1986 LT51780721986315AAA03 | 1987 LT51780721987030AAA03 | 1990 etp178r72_5t19900412 | 1993 LT51780721993158JSA00 | 1996 LT51780721996039JSA00 | 1997 LT51780721997233JSA00 | 1999 LE71780721999263EDC00 | 2000 LE71780722000186EDC00 | 2001 LE71780722001028EDC00 | 2002 elp178r072_7t20010808 | 2003 LE71780722003354ASN01 | 2004 LE71780722004117ASN02 | 2007 Google Inc. | 2011 LT51780712011032JSA00 | 2012 LE71780722012155ASN00 | 2013 Rapid eye | years since cultivation | fallow age (years) | duration of cultivation (years) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 24186 | S | 1 | 0 | 0 | 0 | 0 | 0 | 0.5 | 1 | 1 | 0 | 0 | 0 | 0 | E | 0 | 0 | 0 | 0 | 17.0 | 13 | **4.0** |
| 24188 | S | 2 | 0 | 0 | 0 | 0 | 0 | 0.5 | 1 | 1 | 0.5 | 0 | 0 | 0 | E | 0 | 0 | 0 | 0 | 17.0 | 12 | **5.0** |
| 24190 | S | 2 | | | | | | | | | | | | | | | | | | | | |
| 24184 | S | 3 | 0 | 0 | 0 | 0 | 0 | 0.5 | 1 | 1 | 0 | 0 | 0 | C | E | 0 | 0 | 0 | 0 | 17.0 | 13 | **4.0** |
| 24182 | S | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 1 | 0.5 | 0 | 0 | 0 | E | 0 | 0 | 0 | 0 | 16.0 | 12 | **4.0** |
| 24176 | M | 12 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 1 | 1 | 0.5 | 0 | 0 | E | 0 | 0 | 0 | 0 | 0 | 23 | 13 | **10.0** |
| 24172 | M | 15 | 0 | 0 | 0 | 0.5 | 1 | 0.5 | 1 | 1 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23.0 | 13 | **10.0** |
| 24170 | M | 16 | 0 | 0 | 0 | 0 | 1 | 0.5 | 1 | 0.5 | 0.5 | 0 | 0 | 0 | E | 0 | 0 | 0 | 0 | 20.0 | 13 | **7.0** |
| 24168 | M | 18 | 0 | 0 | 0 | 0.5 | 1 | 0.5 | 1 | 0.5 | 0.5 | 0 | 0 | 0 | E | 0 | 0 | 0 | 0 | 23.0 | 13 | **10.0** |
| 24180 | M | 20 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0.5 | 1 | 0.5 | 0 | 0 | E | E | 0 | 0 | E | 0 | 20.0 | 13 | **7.0** |
| 24156 | L | 21 | 0 | 0.5 | 0.5 | 0.5 | 0.5 | 0 | 0.5 | 1 | 0.5 | 0 | 0 | C | 0 | 0 | 0 | 0 | 0 | 27.0 | 13 | **14.0** |
| 24158 | L | 22 | 0 | 0.5 | 0.5 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | E | 0 | 0 | E | 0 | 27.0 | 13 | **14.0** |
| 24160 | L | 23 | 0 | 0.5 | 0.5 | 0.5 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | E | 0 | 0 | 0 | 0 | 0 | 27.0 | 13 | **14.0** |
| 24164 | L | 24 | 0 | 0.5 | 0.5 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | E | 0 | 0 | 0 | 0 | 0 | 27.0 | 13 | **14.0** |
| 24166 | L | 24 | | | | | | | | | | | | | | | | | | | | |

**Appendix 5.** Vegetation table showing the results of the indicator species analysis for open woodland, dense woodland and the three fallow categories short, medium and long usage. Life form (LF) is given for every species according to Raunkiaer: P = phanerophyte, Ch = chamaephyte, H = hemicryptophyte, Cr = cryptophyte, T = therophyte, brackets indicate uncertain categorization. *Phi* values are given for every species indicating the strength of a species' association to each category or combination of categories. The *phi* value ranges from -1 to 1, however, only significant *phi* values > 0.5 are shown and cells are left empty otherwise. In the case that a species is indicative for more than one category, the highest value is shown in bold. Frequency of occurrence ranges from 1 (low) to 5 (high) and is displayed in the column next to the *phi* values. FNR = field number.

| | LF | Open | | Dense | | Short | | Medium | | Long | | Dense + Short | | Short + Medium | | Short + Medium + Long | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Tephrosia lupinifolia* DC. | Ch | **1.000** | 5 | | | | | | | | | | | | | | |
| *Trachypogon spicatus* (L.f.) Kuntze | H | **0.930** | 5 | | | | | | | | | | | | | | |
| Peeling plane *Ochna pulchra* Hook. | P | **0.905** | 5 | | | | | | | | | | | | | | |
| *Dichapetalum rhodesicum* Sprague & Hutch. | Ch | **0.898** | 5 | | | | | | | | | | | | | | |
| *Schizachyrium jeffreysii* (Hack.) Stapf | H | **0.894** | 5 | | | | | | | | | | | | | | |
| *Chamaecrista* sp. | (T) | **0.873** | 4 | | | | | | | | | | | | | | |
| *Cyperus margaritaceus* Vahl | H | **0.873** | 4 | | | | | | | | | | | | | | |
| *Grewia falcistipula* K.Schum. | P | **0.868** | 5 | | | | | | | | | | | | | | |
| *Diplorhynchus condylocarpon* (Müll.-Arg.) Pichon (Horn-pod tree) | P | **0.843** | 5 | | | | | | | | | | | | | | |
| *Eragrostis cimicina* Launert | (H) | **0.841** | 5 | | | | | | | | | | | | | | |
| *Erythrophleum africanum* (Welw. ex Benth.) Harms (Ordeal tree) | P | **0.831** | 5 | | | | | | | | | | | | | | |
| *Tristachya superba* (De Not.) Schweinf. & Asch. | H | **0.818** | 5 | | | | | | | | | | | | | | |
| *Acrotome* cf. *angustifolia* | T | **0.792** | 5 | | | | | | | | | | | | | | |
| *Asparagus* sp. FNR 133172 | Ch | **0.792** | 5 | | | | | | | | | | | | | | |

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Combretum psidioides* Welw. (Peeling-twig combretum) | P | **0.791** | 5 | | | | | | | | | | | | | | |
| *Pseudolachnostylis maprouneifolia* Pax (Kudu berry) | P | **0.791** | 5 | | | | | | | | | | | | | | |
| *Terminalia brachystemma* Welw. ex Hiern (Kalahari cluster-leaf) | P | **0.765** | 4 | | | | | | | | | | | | | | |
| *Guibourtia coleosperma* (Benth.) J. Léonard (Large false mopane) | P | **0.764** | 5 | | | | | | | | 1 | | | | | | 1 |
| *Perotis leptopus* Pilg. | T | **0.739** | 3 | | | | | | | | | | | | | | |
| *Dialium engleranum* Welw. ex Baker (Kalahari podberry) | P | **0.730** | 4 | | | | | | | | | | | | | | |
| *Aristida stipitata* Hack. | H | **0.724** | 4 | | | | 1 | | 2 | | | | 1 | | 2 | | 1 |
| *Combretum collinum* Fresen. (Bicoloured bushwillow) | P | **0.706** | 5 | | | | | | | | | | | | | | |
| *Tricalysia cacondensis* Hiern | P | **0.706** | 4 | | | | | | | | | | | | | | |
| *Evolvulus alsinoides* (L.) L. (Slender dwarf morning-glory) | Ch | **0.682** | 5 | | | | | | | | | | | | | | |
| *Commelina* sp. FNR 136442 | T | **0.671** | 5 | | | | | | | | | | | | | | |
| *Hymenocardia acida* Tul. | P | **0.634** | 4 | | | | | | | | | | | | | | |
| *Xenostegia tridentata* (L.) D.F.Austin & Staples | Ch | **0.632** | 4 | | | | | | | | 2 | | | | | | 1 |
| *Clerodendrum ternatum* Schinz (Dwarf cat's whiskers) | Ch | **0.624** | 4 | | | | 1 | | | | | | 1 | | 1 | | 1 |
| *Digitaria eriantha* Steud. (Pangola grass) | H | **0.621** | 5 | | | | | | | | | | | | | | |
| *Acrotome inflata* Benth. | T | **0.620** | 3 | | | | | | | | | | | | | | |
| *Indigofera daleoides* Benth. ex Harv. | Cr | **0.582** | 5 | | | | | | | | 2 | | | | | | 1 |
| *Lannea gossweileri* ssp. *gossweileri* Exell & Mendonça | Ch | **0.560** | 3 | | | | | | | | | | | | | | |

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Baikiaea plurijuga* Harms (Zambezi teak) | P | | 3 | **0.948** | 5 | | 4 | | 4 | | 4 | 0.557 | 5 | | 4 | | 4 |
| *Commiphora tenuipetiolata* Engl. (Satin-bark corkwood) | P | | | **0.782** | 5 | | 4 | | 3 | | 1 | 0.528 | 5 | | 4 | | 3 |
| *Erythrococca menyharthii* (Pax) Prain (Northern red-berry) | P | | | **0.769** | 5 | | 1 | | 2 | | | 0.616 | 3 | | 2 | | 1 |
| *Asystasia gangetica* (L.) T.Anderson (Creeping foxglove) | Ch | | 1 | **0.739** | 4 | | 1 | | 1 | | 1 | | 3 | | 1 | | 1 |
| *Alectra picta* (Hiern) Hemsl. | T | | | **0.739** | 3 | | | | | | | | 2 | | | | |
| *Apocynaceae* sp. FNR 136422 | Ch | | 4 | **0.718** | 4 | | | | 3 | | | | 2 | | 2 | | 1 |
| *Combretum celastroides* Welw. ex M.A. Lawson (Jesse-bush bushwillow) | P | | | **0.708** | 5 | | 5 | | 5 | | 5 | 0.520 | 1 | | 1 | | 5 |
| Climber FNR 136421 | Ch | | | **0.651** | 4 | | | | | | | | 2 | | | | |
| *Ocimum* sp. FNR 136406 | T | | | **0.624** | 4 | | | | 1 | | | | 2 | | 1 | | 1 |
| *Commelina* sp. FNR 136400 | T | | | **0.620** | 3 | | | | | | | | 2 | | | | |
| *Panicum maximum* Jaq. (Guinea grass) | H | | | **0.615** | 5 | | 1 | | 2 | | 1 | | 3 | | 2 | | 2 |
| Creeper FNR 136404 | Ch | | | **0.611** | 4 | | | | 1 | | | | 2 | | 1 | | 1 |
| *Grewia flavescens* Juss. (Sandpaper raisin) | P | | | **0.605** | 4 | | 1 | | 2 | | | | 3 | | 2 | | 1 |
| *Croton gratissimus* Burch. (Lavender croton) | P | | | **0.600** | 5 | | 5 | | 5 | | 5 | | 1 | | 1 | | 5 |
| *Combretum engleri* Schinz | P | | | **0.580** | 5 | | 5 | | 5 | | 5 | | 1 | | 1 | | 5 |
| *Ipomoea dichroa* Choisy | T | | | **0.576** | 5 | | 3 | | 3 | | 3 | | 4 | | 3 | | 3 |
| *Hibiscus* cf. *mastersianus* FNR 136278 | T | | 2 | **0.557** | 5 | | 4 | | 5 | | 5 | | 5 | | 5 | | 5 |
| *Berchemia* cf. *discolor* FNR 136423 | P | | | **0.551** | 4 | | | | 1 | | | | 2 | | 1 | | 1 |
| *Fabaceae* sp. FNR 136412 | P | | | | 4 | **0.815** | 5 | | 4 | | | 0.584 | 5 | 0.549 | 5 | | 3 |
| *Cyanotis foecunda* Hassk. | T | | | | 5 | **0.800** | 5 | | 5 | | 4 | 0.710 | 1 | | 1 | | 5 |
| *Panicum* sp. FNR 136397 | (H) | | | | 3 | **0.770** | 5 | | 5 | | 2 | | 4 | 0.541 | 1 | | 4 |
| *Hermannia eenii* Baker | Ch | | 1 | | | **0.631** | 3 | | 1 | | 1 | | 2 | | 2 | | 2 |

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Climber FNR 136408 | Ch | | | | 4 | **0.614** | 4 | | 3 | | 1 | 0.546 | 4 | | 4 | | 3 |
| *Ochna afzelii ssp. mechowiana* R.Br. ex Oliv. | P | | | | 5 | **0.586** | 4 | | 1 | | 1 | | 5 | | 3 | | 2 |
| Malvaceae sp. FNR 136225 | (Ch/T) | | | | | **0.540** | 5 | | 1 | | | | 3 | | 3 | | 2 |
| *Justicia bracteata* (Hochst.) Zarb | Ch | | 1 | | 5 | | 5 | **0.754** | 5 | | 4 | | 1 | | 1 | | 5 |
| *Clerodendrum uncinatum* Schinz | Ch | | | | | | 1 | **0.639** | 4 | | 1 | | 1 | | 3 | | 2 |
| Asteraceae sp. FNR 136391 | (T) | | | | | | 3 | **0.623** | 4 | | 1 | | 2 | | 4 | | 3 |
| *Digitaria ciliaris* (Retz.) Koeler (Southern crabgrass) | H | | | | | | 2 | | | **0.655** | 4 | | 1 | | 1 | | 2 |
| *Chamaecrista biensis* (Steyaert) Lock | (T/Ch) | | | | 1 | | 1 | | | **0.639** | 4 | | 1 | | 1 | | 2 |
| *Acanthosicyos naudinianus* (Sond.) C.Jeffrey (Gemsbok cucumber) | Ch | | | | | | 2 | | 5 | **0.560** | 5 | | 1 | | 4 | | 4 |
| *Chamaecrista absus* (L.) Irwin & Barneby | T | | 3 | | | | | | 2 | **0.533** | 4 | | | | 1 | | 2 |
| Lanzettblatt Fr. rot (Munkudi) 136374 | P | | | | 3 | 0.558 | 5 | | 4 | | 2 | **0.574** | 4 | | 5 | | 4 |
| *Dichrostachys cinerea* (L.) (Sicklebush) | P | | | | 1 | | 5 | | 5 | | 3 | | 3 | **0.691** | 1 | | 5 |
| *Acacia ataxacantha* DC. (Flame thorn) | P | | | | 5 | | 5 | | 5 | | 4 | | 1 | **0.621** | 1 | | 5 |
| *Baphia massaiensis* Taub. (Jasmine pea) | P | | | | 5 | 0.501 | 5 | | 5 | | 5 | | 1 | **0.603** | 1 | 0.601 | 5 |
| *Urochloa brachyura* (Hack.) Stapf | T | | | | 3 | | 5 | | 5 | | 5 | | 4 | **0.583** | 1 | 0.568 | 5 |
| *Setaria pumila* (Poir.) Roem. & Schult. | (T) | | 1 | | 5 | | 5 | | 5 | | 3 | | 1 | **0.552** | 1 | | 5 |
| *Eragrostis cylindriflora s.lat.* | H | | | | | | 5 | 0.521 | 5 | | 5 | | 3 | 0.617 | 1 | **0.648** | 5 |
| *Grewia retinervis* Burret | P | | | | 2 | | 5 | | 4 | | 5 | | 4 | | 5 | **0.577** | 5 |

**APPENDIX 6.** Pearson correlation of the variables with the first three axes of the Principal Component Analysis. R values shown; Soil depths: H1 = 0–10 cm, H2 = 25–45 cm, H3 = 70–90 cm, H4 = 180–200 cm.

| PCA name | Variable | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|---|
| TotalCov | Total Cover | 0.278 | 0.645 | 0.103 |
| 0.0-0.5m | 0.0-0.5 m Cover | -0.545 | 0.473 | 0.109 |
| 1-2m | 1-2 m Cover | 0.634 | 0.592 | -0.128 |
| 2-5m | 2-5 m Cover | 0.832 | 0.126 | -0.069 |
| 5-10m | 5-10 m Cover | 0.624 | -0.377 | 0.016 |
| 10-20m | 10-20 m Cover | 0.431 | -0.334 | -0.121 |
| MainHeig | Height of the lowest 95 % | 0.510 | -0.489 | -0.241 |
| FireCat | Fire category | 0.716 | 0.325 | -0.004 |
| LAI130 | Leaf Area Index 130 cm | 0.912 | 0.130 | -0.057 |
| Woodlitt | Woody litter Cover | 0.263 | -0.252 | -0.076 |
| Softlitt | Soft litter Cover | 0.690 | 0.000 | -0.326 |
| Moss | Mosses Cover | 0.695 | 0.044 | -0.180 |
| Lichen | Lichen Cover | 0.507 | 0.029 | -0.257 |
| Grazing | Grazing signs | -0.337 | -0.823 | -0.218 |
| BA<5cm | Basal Area for DBH < 5cm | 0.687 | 0.259 | -0.120 |
| BA>5cm | Basal Area for DBH > 5cm | 0.627 | -0.400 | -0.198 |
| ConductH1 | Conductivity H1 | 0.519 | 0.216 | 0.013 |
| LimeH1 | Lime content H1 | -0.177 | -0.102 | -0.062 |
| ClayH1 | Clay content H1 | 0.429 | 0.199 | 0.744 |
| SiltH1 | Silt content H1 | -0.231 | -0.034 | 0.373 |
| SandH1 | Sand content H1 | -0.202 | -0.131 | -0.739 |
| pHCaClH1 | pH in $CaCl_2$ H1 | -0.688 | 0.449 | 0.144 |
| KH1 | Potassium content H1 | 0.068 | 0.783 | -0.487 |
| NaH1 | Sodium content H1 | 0.400 | 0.391 | -0.159 |
| CaH1 | Calcium content H1 | -0.501 | 0.602 | -0.340 |
| MgH1 | Magnesium content H1 | -0.010 | 0.524 | -0.106 |
| PH1 | Phosphorus content H1 | -0.116 | 0.219 | -0.330 |
| ALHH1 | Aluminium hydride content H1 | 0.273 | -0.400 | -0.199 |
| FluoriH1 | Fluoride content H1 | 0.237 | -0.056 | -0.150 |
| ChloriH1 | Chloride content H1 | 0.189 | -0.022 | -0.494 |
| NitratH1 | Nitrate content H1 | 0.463 | 0.204 | -0.309 |
| SulphaH1 | Sulphate content H1 | -0.097 | 0.561 | 0.044 |
| AmoniuH1 | Ammonium content H1 | 0.261 | 0.383 | 0.351 |
| ConductH2 | Conductivity H2 | 0.326 | 0.436 | 0.290 |
| PCA name | Variable | Axis 1 | Axis 2 | Axis 3 |

| | | | | |
|---|---|---|---|---|
| LimeH2 | Lime content H2 | -0.174 | 0.195 | -0.048 |
| ClayH2 | Clay content H2 | 0.522 | 0.035 | 0.467 |
| SiltH2 | Silt content H2 | 0.149 | 0.168 | 0.379 |
| SandH2 | Sand content H2 | -0.450 | -0.103 | -0.515 |
| pHCaClH2 | pH in CaCl2 H2 | -0.679 | 0.513 | 0.169 |
| KH2 | Potassium content H2 | 0.381 | 0.611 | -0.448 |
| NaH2 | Sodium content H2 | 0.196 | 0.439 | -0.312 |
| CaH2 | Calcium content H2 | -0.382 | 0.625 | -0.198 |
| MgH2 | Magnesium content H2 | 0.036 | 0.741 | -0.073 |
| PH2 | Phosphorus content H2 | -0.381 | 0.255 | -0.419 |
| ALHH2 | Aluminium hydride content H2 | 0.553 | -0.262 | -0.089 |
| FluoriH2 | Fluoride content H2 | -0.034 | -0.559 | -0.155 |
| ChloriH2 | Chloride content H2 | 0.362 | 0.008 | 0.010 |
| NitratH2 | Nitrate content H2 | 0.431 | -0.106 | -0.427 |
| SulphaH2 | Sulphate content H2 | -0.007 | 0.351 | 0.189 |
| AmoniuH2 | Ammonium content H2 | 0.281 | -0.094 | 0.486 |
| ConductH3 | Conductivity H3 | 0.257 | 0.413 | 0.615 |
| LimeH3 | Lime content H3 | -0.067 | 0.308 | -0.108 |
| ClayH3 | Clay content H3 | 0.469 | 0.381 | 0.582 |
| SiltH3 | Silt content H3 | 0.629 | 0.214 | 0.154 |
| SandH3 | Sand content H3 | -0.689 | -0.354 | -0.421 |
| pHCaClH3 | pH in CaCl2 H3 | -0.674 | 0.362 | 0.175 |
| KH3 | Potassium content H3 | 0.307 | 0.687 | -0.453 |
| NaH3 | Sodium content H3 | 0.271 | 0.158 | -0.316 |
| CaH3 | Calcium content H3 | -0.285 | 0.565 | -0.225 |
| MgH3 | Magnesium content H3 | -0.233 | 0.565 | -0.468 |
| PH3 | Phosphorus content H3 | -0.212 | 0.243 | -0.255 |
| ALHH3 | Aluminium hydride content H3 | 0.467 | -0.415 | -0.350 |
| FluoriH3 | Fluoride content H3 | 0.138 | -0.340 | -0.493 |
| ChloriH3 | Chloride content H3 | 0.109 | 0.238 | -0.037 |
| NitratH3 | Nitrate content H3 | 0.089 | 0.222 | -0.599 |
| SulphaH3 | Sulphate content H3 | -0.065 | -0.020 | 0.464 |
| AmoniuH3 | Ammonium content H3 | 0.024 | -0.270 | 0.255 |
| ConductH4 | Conductivity H4 | 0.036 | 0.308 | 0.434 |
| LimeH4 | Lime content H4 | -0.201 | 0.109 | 0.083 |
| ClayH4 | Clay content H4 | 0.402 | 0.381 | 0.189 |
| SiltH4 | Silt content H4 | 0.544 | 0.263 | 0.190 |
| SandH4 | Sand content H4 | -0.652 | -0.408 | -0.246 |
| pHCaClH4 | pH in CaCl2 H4 | -0.553 | 0.327 | 0.268 |
| KH4 | Potassium content H4 | 0.089 | 0.788 | -0.484 |

| PCA name | Variable | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|---|
| NaH4 | Sodium content H4 | 0.363 | 0.453 | -0.252 |
| CaH4 | Calcium content H4 | -0.344 | 0.626 | -0.253 |
| MgH4 | Magnesium content H4 | -0.418 | 0.439 | -0.155 |
| PH4 | Phosphorus content H4 | -0.589 | 0.082 | -0.098 |
| ALHH4 | Aluminium hydride content H4 | 0.036 | -0.083 | 0.314 |
| FluoriH4 | Fluoride content H4 | 0.113 | -0.374 | -0.467 |
| ChloriH4 | Chloride content H4 | 0.465 | -0.025 | -0.305 |
| NitratH4 | Nitrate content H4 | 0.051 | 0.099 | -0.530 |
| SulphaH4 | Sulphate content H4 | 0.126 | 0.019 | 0.386 |
| AmoniuH4 | Ammonium content H4 | -0.085 | -0.286 | 0.377 |