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ERRATUM

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In Table 1, on page 7, please read “Oleaceae” in place of “Olacaceae”. The authors regret this error.

The original, unaltered publication begins on the following page.

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Woody species of the Miombo woodlands and geoxylic grasslands of the Cusseque area, south-central Angola

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Abstract: The species composition of the vegetation in most regions of Angola has been poorly studied and most studies date back to the pre-independence era. In this study, we provide a detailed account of the woody flora of the Miombo woodlands and geoxylic grasslands of the Cusseque study site of "The Future Okavango" (TFO) project, situated on the Angolan Central Plateau. The checklist is based on a vegetation survey using vegetation plots of 1,000 m^2 and also includes records from botanical collections made elsewhere at the study site. In total, we documented 154 woody species belonging to 99 genera of 37 plant families in 100 km^2. The study represents the first comprehensive account of the woody vegetation of the area including all habitats and growth forms.

Key words: Angola; Bié; geoxylic suffrutex; Miombo; The Future Okavango project; vegetation survey

INTRODUCTION

Rural communities in Angola hold an enormous knowledge of the local flora and especially have great understanding of the potential usages of plants (Figueiredo & Smith 2012; Kissanga 2016). In contrast, scientific exploration and documentation of the vegetation of Angola is still limited. Early botanists such as Friedrich Welwitsch visited the country in the middle of the 19th century (Welwitsch 1869). The most influential botanist working in Angola in the first half of the 20th century was John Gossweiler, who worked in all Angolan provinces and collected over 14,000 specimens. His collection is considered an especially important source of information for rare and endemic species (Figueiredo & Smith 2008). Furthermore, Gossweiler produced the first phytogeographic map of Angola containing 19 principal vegetation types (Gossweiler & Mendonça 1939). Based on this map and his own observations, Luís A. Grandvaux Barbosa published a new phytogeographic map in 1971 containing 32 main types and over 100 subordinate types dealt with in the text (Barbosa 1970, 1971). However, the descriptions of these vegetation types were of general character and limited to the dominant species. Detailed descriptions of the species composition and plant diversity of the Angolan vegetation are lacking for most parts of the country. For the province of Bié, Monteiro (1970) provided an excellent overview on the woody vegetation including the first provincial map of the woodlands. Based on 144 relevés, Monteiro delineated three associations of woody plants and four sub-associations.

The civil war that followed Angola's independence in 1975 made any scientific work in Angola extremely difficult, and thus, most scientific literature available today dates back to the pre-independence era. Since the end of the armed conflict in 2002, scientific work is slowly increasing. However, botanical work in the country is still hampered by the lack of field guides and the fact that the principal work on the flora of Angola, the *Conspectus Florae Angolensis,* remains unfinished and important families such as the Rubiaceae are not treated. Similarly, a countrywide checklist of the flora of Angola was lacking until the recent publication of "Plants of Angola – Plantas de Angola" by Figueiredo & Smith (2008). Nevertheless, inventories of vascular plants at the local and regional scale are still lacking for most parts of the country. Such inventories are indispensable for any kind of natural resource management planning, conservation measures or ecological studies (Figueiredo et al. 2009).

The interdisciplinary research project "The Future Okavango" (TFO) aims to provide a scientific basis for strategic resource planning for the Okavango Basin. The headwaters of the Okavango River, where 95% of the runoff are generated, are located on the Angolan Central Plateau (Steudel et al. 2013). Rapid transformations of the social-ecological systems are currently taking place there (Pröpper et al. 2015). However, little knowledge

and data on the vegetation and the botanical diversity was available (Revermann 2016). In this study, we present results of the vegetation survey carried out at the research site "Cusseque" in the province of Bié located at the upper reaches of the Okavango River.

MATERIALS AND METHODS

Study site

The Okavango River originates on the Angolan Central Plateau and terminates in a large inland delta in the Kalahari Desert in Botswana. Within the TFO project, detailed studies were carried out at four research sites representing the different parts of the river basin. The work presented in this paper was carried out at the study site Cusseque with an area of 100 km^2 (13.6985° S, 017.0382° E). The site is located on the Angolan Central Plateau in the province of Bié (Figure 1; Wehberg & Weinzierl 2013). The landscape can be described as a rolling plain intersected by the Cusseque River and its many tributaries, which are orientated perpendicular to each other. Three major landscape units can be identified: the elevated areas, the sloping areas leading down to the valley bottoms and the valley floors (Gröngröft et al. 2013b). The mean elevation is 1,575 m above sea level while the difference in elevation between the valley bottom of the main river and the surrounding elevated areas is about 100 m (Gröngröft et al. 2013b). The climate of the Cusseque area is semi-humid with a pronounced wet season lasting from November to April. The mean annual precipitation is 987 mm and the mean annual temperature is 20.4°C (Weber 2013). The study area harbours a high pedodiversity. The elevated areas are characterized by deep and developed slightly loamy Arenosols. The slopes of the smaller valleys of the tributaries and at the western side of the Cusseque River show shallow Plinthisols on granitic bedrock. The soils along the eastern part of the Cusseque River are characterized by very deep and leached Arenosols. The centre of the valleys support Histosols with peat layers exceeding 1 m in depth while at the edges of the wetlands Gleysols are the common soil type (Gröngröft et al. 2013a).

The main vegetation types covering south central Angola are semi-deciduous Miombo woodlands and forests (Figures 2a and b). These woodlands are interspersed with open vegetation types locally termed *anharas de ongote*. The salient feature of the open vegetation types are dwarf shrubs with a huge underground woody biomass. This distinct life form was described by White (1976) as "geoxylic suffrutex". In the Cusseque area, geoxylic suffrutices occur on two different soil types: on deep, leached sandy soils and on shallow, compact, ferralitic soils. Accordingly, we will differentiate herein between "geoxylic grasslands on sandy soils" (Figure 2c) and "geoxylic grasslands on ferralitic soils" (Figure 2d). The occurrences of the different vegetation types are governed by topography: woodlands and forests are confined to the elevated areas and upper slopes. The mid- and lower

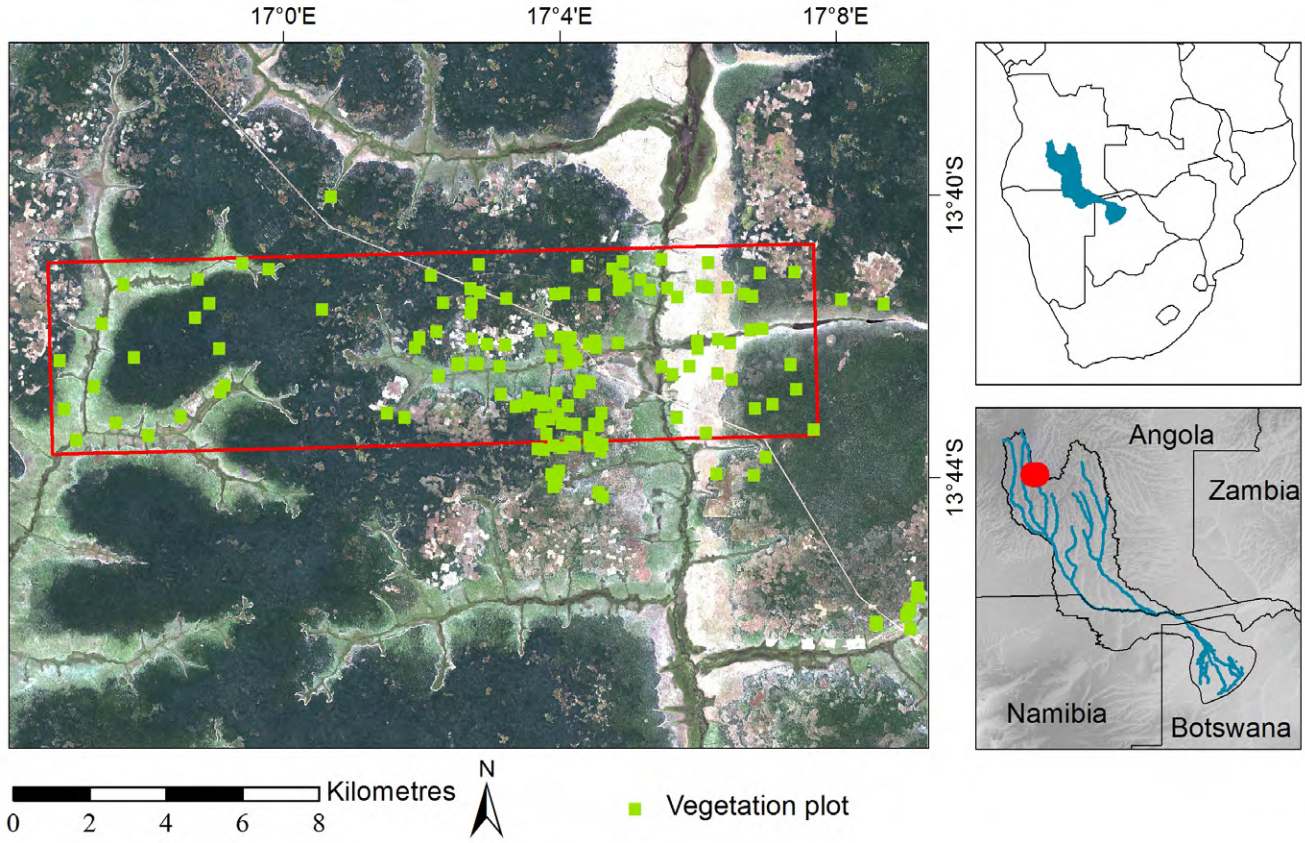

Figure 1. Location of the Okavango Basin in southern Africa and the study site "Cusseque" denoted in red. (Projection: WGS 1984; background: RapidEye high-resolution satellite imagery, recorded 1 May 2013. We acknowledge the DLR for the provision of the data from the RapidEye Science Archive.)

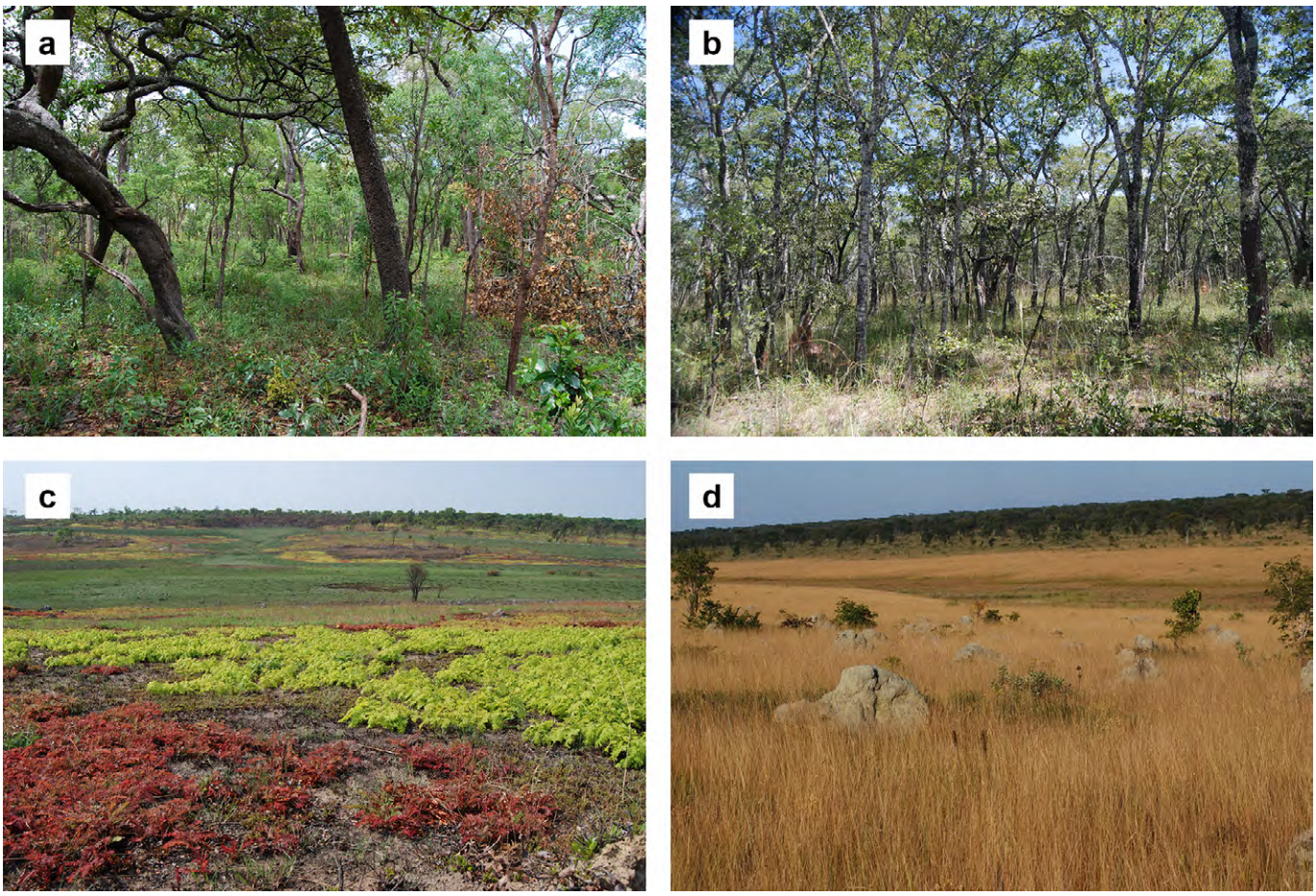

Figure 2. Landscapes of the Cusseque study area: **a)** Miombo woodland in the middle of the rainy season, **b)** Miombo woodland at the end of the rainy season, **c)** geoxylic grasslands dominated by *Cryptosepalum maraviense* at the beginning of the rainy season in October, **d)** geoxylic grassland on sandy soils at the beginning of the dry season in May; in the background wetland on the valley bottom and Miombo woodlands.

slopes feature geoxylic grasslands. The woodlands and geoxylic grasslands are separated by ecotones extending up to several hundred meters where elements of both vegetation types co-occur. The valley bottoms support wetlands dominated by Cyperaceae (Revermann et al. 2013; Schneibel et al. 2013).

Data collection

Plot based vegetation surveys were carried out during the growing season in the years 2011 to 2014 and all information is stored in the Vegetation Database of the Okavango Basin (GIVD ID: AF-00-009, Revermann et al. 2016). In order to evenly map all existing vegetation units, sampling followed a random, stratified design. Based on an image segmentation algorithm using all bands of a Landsat 7 scene, seven major vegetation units were identified. In these vegetation units random points were created using GIS and transferred to a hand-held GPS for localization in the field. Furthermore, additional vegetation plots were examined in different successional stages of Miombo forest to analyse successional pathways of the regeneration of natural vegetation after disturbance by shifting cultivation (Gonçalves et al., accepted). We used a nested plot design with a 10 m × 10 m plot located in the centre of a 20 m × 50 m plot. In total, we sampled 148 vegetation plots. Due to the unique character of the geoxylic grasslands, these were subject to an additional field study. Therein, data were collected using 10 m × 10 m plots with two 3.3 m × 3.3 m subplots situated in diagonally opposite corners (adapted from Dengler 2009). In every plot all vascular plants found were recorded and their projected cover estimated visually. Unknown plants were photographed and voucher specimens were collected according to botanical methods outlined by Victor et al. (2004). Voucher specimens were deposited in the herbarium of the ISCED Huíla (LUBA) and in the Herbarium Hamburgense (HBG). In addition to the species recorded on the vegetation plots, species found elsewhere while working at the study area were added to the checklist. A high number of vegetation plots and several months of field work carried out by four observers in all seasons ensured a comprehensive coverage of the woody species present at the study area.

Taxonomy and plant identification

We followed the taxonomy of the checklist "Plants of Angola – Plantas de Angola" by Figueiredo & Smith (2008). We are aware of recent changes in the taxonomy, but decided to conform to the national checklist. For identification, we consulted the *Conspectus Florae Angolensis* (Exell & Mendonça 1937, 1951, 1954, 1955; Exell & Fernandes

1962, 1966; Exell et al. 1970) when possible, and the flora of neighbouring countries, especially the *Flora Zambeziaca* (Exell & Wild 1960) and the field guide to the *Trees and shrubs of Namibia* (Mannheimer & Curtis 2009). Additionally, we consulted herbarium collections at the ISCED Huíla (LUBA) and the Instituto de Investigação Científica Tropical (LISC) as well as the on-line database JSTOR Plant Science (http://plants.jstor.org/). For some specimens, we consulted experts at Kew Botanical Garden (K).

Permits

Permits for plant collection and transfer of biological material in Angola for scientific purposes was arranged based on the framework of Material Transfer Agreements from Angola, negotiated between the Instituto Superior de Ciências de Educação da Huíla (ISCED, Huíla), Lubango and the University of Hamburg (UHH), Germany and authorized on behalf of the Angolan Government by the Director for Agriculture, Fisheries and Environment of the Province of Huíla. All International Conventions to which Angola is signatory country, such as Convention on International Trade in Endangered Species of Wild Fauna and Flora (1973), Convention on Biological Diversity (1992), International Treaty on Plant Genetic Resources for Food and Agriculture (2004), and all other relevant national and international instruments concerning biodiversity were taken into account.

Data analysis

We visualized the number of species per family of all species belonging to one family using the function 'pie' in the statistical software R (R Development Core Team 2016). Data on the frequency of occurrence of a species, the habitat and the life form were compiled from vegetation plot data. We assigned frequency according to the following categories: very rare (1 or 2 observations), rare (3–5 observations), occasional (6–10 observations), frequent (11–30 observations), common (>30 observations). We assigned every species to one or more of the following life form categories based on field observations and literature: tree, shrub, liana, dwarf shrub and geoxyle. For geoxyles we followed the definition proposed by White (1976). White defined a geoxyle as a dwarf shrub that has closely related species growing as trees and that exhibits massive woody underground parts.

RESULTS

We documented 154 woody species belonging to 99 genera and 37 families (Table 1). The majority of species belonged to the family Fabaceae (33), followed by Rubiaceae (22), Euphorbiaceae (11), Proteaceae (10) and Combretaceae (9) (Figure 3). Most of the dominant species belonged to the Fabaceae and occurred with high frequencies. In contrast, the Rubiaceae, second in species richness, contained species occurring with low frequencies and were less abundant. The woodlands and forests showed the highest woody species richness with 110 species belonging to 32 families. A surprisingly high number of 33 woody species from 14 families were found in the geoxylic grasslands. These open vegetation types appear to be merely grasslands in the late growing season (Figures 2c and d) but in fact harbour a remarkable diversity of woody species (Table 1). In the wetlands few woody species occurred and we recorded only two *Ficus* species sporadically occurring along the margins of the wetlands.

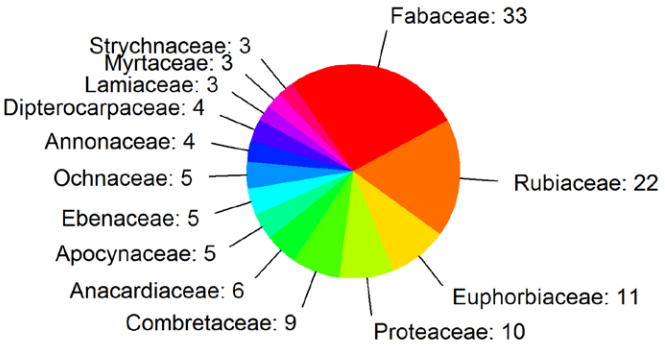

Figure 3. The families of woody plants found at the Cusseque study site, south-central Angola. Only families with more than two species are shown. In total 37 families of woody plant species occurred, containing 154 species in 99 genera.

One species, *Combretum schumannii* Engl., was recorded but is not listed in the current checklist of Angola (Figueiredo & Smith 2008).

DISCUSSION

The 154 species recorded within the 100 km^2 of the Cusseque study site almost equalled the 166 woody species found by Monteiro (1970) in the entire province of Bié, an area of 70,314 km^2. This does not reflect the quality of the study of Monteiro but rather illustrates how poorly the region has been surveyed so far. In fact, the study carried out by Monteiro (1970) is of high quality and stands out as the only study of its time from Angola basing its analysis on quantitative, plot based data. However, the study was restricted to woodlands and only larger shrubs and trees were included. In contrast, we included all vegetation types ranging from woodlands to geoxylic grasslands and wetlands. Due to the high sampling intensity and the coverage of all vegetation types our species list can therefore be considered a comprehensive checklist of the woody plant species of the Cusseque area. However, it must be noted that this list does not contain any specimen that could not be identified to at least genus level; some specimens were lacking fruits or flowers, preventing further identification. Therefore, the actual number of woody species may be slightly higher.

Despite the relatively recent publication of the checklist of vascular plants of Angola, subsequent field surveys in various parts of the country have resulted in additions to the checklist (Huntley & Coelho 2011). We provided the first record in Angola of the herbaceous Asteraceae *Schistostephium crataegifolium* (DC.) Fenzl ex Harv, during the

Table 1. List of species arranged by family. Voucher specimens have been deposited in the herbaria of Lubango (LUBA) and Hamburg (HBG). In most cases doublets are stored in both herbaria. The herbarium name in parentheses is the location where the specimen used for identification is deposited. Frequency was assigned according to the following categories: very rare (1 or 2 observations), rare (3–5 observations), occasional (6–10 observations), frequent (11–30 observations), common (>30 observations). Life forms of the species were assigned to one or more of the categories: tree, shrub, liana, dwarf shrub and geoxyle.

Species name	Frequency	Life form	Habitat	Collection number(s)
Anacardiaceae				
Ozoroa cf. xylophylla (Engl. &Gilg) R.Fern. & A.Fern.	very rare	shrub	geoxylic grassland (sandy soils)	133057B (HBG)
Ozoroa stenophylla Engl. & Gilg.	frequent	shrub	woodland / grassland (ferralitic soils)	140123 (LUBA)
Rhus arenaria Torre, A.R.	frequent	dwarf shrub / geoxyle	geoxylic grassland (ferralitic soils)	140101 (LUBA)
Rhus exelliana Meikle	frequent	dwarf shrub		135250; 134275 (HBG)
Rhus gracilipes Exell	frequent	dwarf shrub	woodland / forest	139227; 132483 (HBG)
Rhus kirkii Oliv.	frequent	dwarf shrub	woodland / forest	139253 (LUBA)
Anisophylleaceae				
Anisophyllea boehmii Engl.	frequent	tree	woodland / forest	134316; 139018; 135297 (HBG)
Anisophyllea quangensis Engl. ex Henriq.	rare	dwarf shrub	geoxylic grassland (sandy soils)	133044; 134116 (HBG); 140109 (LUBA)
Annoncaceae				
Annona stenophylla ssp. *nana* Engl. & Diels	rare	dwarf shrub	woodland / forest	133058; 134218 (HBG); 140065 (LUBA)
Uvaria angolensis Welw. ex Oliv. (Figure 4b)	frequent	shrub	woodland / forest	135323; 134240 (HBG)
Xylopia odoratissima Welw. ex Oiv.	frequent	shrub	woodland / forest	133057A; 134263 (HBG)
Xylopia tomentosa Exell	common	shrub	woodland / forest	135279; 132956; 132986 (HBG); 139177 (LUBA)
Apocynaceae				
Chamaeclitandra henriquesiana (Hallier f.) Pichon	common	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140121 (LUBA)
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	frequent	shrub / tree	woodland / forest	135300 (HBG)
Landolphia camptoloba (K.Schum.) Pichon	frequent	liana	woodland / forest	132537 (HBG)
Landolphia gossweileri (Stapf) Pichon	rare	dwarf shrub	geoxylic grassland (sandy soils)	133048 (HBG)
Strophanthus welwitschii (Baill.) K.Schum.	frequent	liana	woodland / forest	135336; 135378; 134091 (HBG)
Asparagaceae				
Asparagus sp. 135286	frequent	shrub	woodland / forest	135286 (HBG)
Asparagus cf. *africanus* Lam.	very rare	shrub	woodland / forest	134115 (HBG)
Asteraceae				
Helichrysum krausii Sch. Bip	occasional	shrub	woodland / forest	132695 (HBG)
Crysobalanaceae				
Parinari capensis Harv.	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	132664; 132898; 140068 (HBG)
Parinari curatellifolia Planch. ex Benth.	common	tree	woodland / forest	132444 (HBG)
Combretaceae				
Combretum acutifolium Exell	very rare	liana / shrub	woodland / forest	135306 (HBG)
Combretum collinum Fresen.	common	tree	woodland / forest	139176 (HBG)
Combretum elaeagnoides Klotzsch	very rare	tree	woodland / forest	132538 (HBG)
Combretum engleri Schinz	frequent	shrub	woodland / forest	133216 (HBG)
Combretum platypetalum ssp. *platypetalum* Welw. ex M.A.Lawson (Figure 4f)	occasional	dwarf shrub	geoxylic grassland (sandy soils)	132639; 134114; 140113 (HBG)
Combretum schumannii Engl.	rare	shrub	woodland / forest	139048 (LUBA)
Combretum zeyheri Sond.	frequent	shrub / tree	woodland / forest	135280; 132510 (HBG)
Pteleopsis anisoptera (Welw.) Engl. & Diels	frequent	shrub / tree	woodland / forest	135365; 134110 (HBG); 139066 (LUBA)
Terminalia brachystemma Welw. ex Hiern	frequent	tree	woodland / forest / grassland (sandy and ferralitic soils)	132997; 134088; 134131 (HBG)
Dichapetalaceae				
Dichapetalum cymosum (Hook.) Engl.	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140165 (LUBA)
Dipterocarpaceae				
Monotes africanus A.DC.	common	tree	woodland / forest	132917; 134160; 134228 (HBG)
Monotes angolensis de Wild.	very rare	tree	woodland / forest	132443 (HBG)
Monotes caloneurus Gilg.	rare	tree	woodland / forest	134820 (HBG)
Monotes dasyanthus Gilg	common	tree	woodland / forest	132907; 132961 (HBG); 139228 (LUBA)
Ebenaceae				
Diospyros batocana Hiern	occasional	shrub / tree	woodland / forest	139247 (LUBA)
Diospyros chamaethamnus Dinter ex Mildbr.	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140179 (LUBA)

Continued

Table 1. *Continued.*

Species name	Frequency	Life form	Habitat	Collection number(s)
Ebenaceae, *continued*				
Diospyros pseudomespilus ssp. *brevicalyx* Mildbr.	frequent	shrub	woodland / forest	135379 (HBG)
Diospyros virgata (Gürke) Brenan	occasional	shrub	woodland / forest	132941 (HBG)
Euclea crispa ssp. *crispa* (Thunb.) Gürke	frequent	dwarf shrub	woodland / forest / geoxylic grassland	135413 (HBG)
Ericaceae				
Erica benguellensis (Welw. ex Engl.) E.G.H. Oliv.	very rare	shrub / tree	woodland / forest	139235 (LUBA)
Euphorbiaceae				
Bridelia sp. 139095	occasional	shrub / tree	woodland / forest	139095 (LUBA)
Hymenocardia acida Tul.	frequent	shrub / tree	woodland / forest	134099; 134135 (HBG); 139068 (LUBA)
Maprounea africana Müll. Arg.	rare	shrub / tree	woodland / forest	139113 (LUBA)
Phyllanthus angolensis Müll. Arg.	rare	dwarf shrub	woodland / forest	139256 (LUBA)
Phyllanthus sp. 139238	common	dwarf shrub	woodland / forest	139238 (LUBA)
Phyllanthus welwitschianus Müll. Arg.	common	dwarf shrub	woodland / forest	139237 (LUBA)
Pseudolachnostylis maprouneifolia Pax	occasional	tree	woodland / forest	132555; 134232 (HBG); 139038 (LUBA)
Sclerocroton oblongifolius (Müll. Arg.) Kruijt & Roebers	frequent	dwarf shrub	woodland / forest	132990; 134185 (HBG)
Uapaca sp. 134199	common	dwarf shrub / geoxyle	geoxylic grassland (ferralitic soils)	132490; 134199 (HBG)
Uapaca kirkiana Müll. Arg.	common	tree	woodland / forest	-
Uapaca nitida var. *nitida* Müll. Arg.	common	tree	woodland / forest	132691; 132912; 132998 (HBG)
Fabaceae				
Abrus melanospermus ssp. *suffruticosus* (Boutique) D.K.Harder	occasional	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140167 (LUBA)
Albizia antunesiana Harms	frequent	tree	woodland / forest	134156; 135318 (HBG); 139223 (LUBA)
Albizia gummifera (J.F.Gmel) C.A.Sm.	occasional	shrub / tree	woodland / forest	139065; 135342; 132967 (HBG)
Baphia bequaertii De Wild.	frequent	shrub / tree	woodland / forest	135360; 139242; 133018 (HBG)
Bauhinia petersiana Bolle	common	shrub	woodland / forest	135311 (HBG)
Bobgunnia madagascariensis (Desv.) J.H.Kirkbr. & Wiersema	frequent	shrub / tree	woodland / forest	132963; 139128 (LUBA)
Brachystegia bakeriana Hutch. & Burtt Davy	common	tree	woodland / forest	135298; 139016 (LUBA)
Brachystegia longifolia Benth.	occasional	tree	woodland / forest	132957; 139255 (LUBA)
Brachystegia spiciformis Benth.	common	tree	woodland / forest	132676 (HBG)
Burkea africana Hook.	common	tree	woodland / forest	-
Copaifera baumiana Harms	common	shrub	woodland / forest	132900; 135335 (HBG); 139233 (LUBA)
Crotalaria amoena Welw. ex Baker	rare	dwarf shrub	woodland / forest	139121 (LUBA)
Crotalaria cistoides Welw. ex Baker	rare	dwarf shrub	woodland / forest	139257 (LUBA)
Crotalaria florida Welw. ex Baker	rare	dwarf shrub	woodland / forest	139196 (LUBA)
Cryptosepalum exfoliatum ssp. *pseudotaxus* (Baker f.) P.A.Duvign. & Brenan (Figure 4i)	common	tree	woodland / forest	135304 (HBG); 139023 (LUBA)
Cryptosepalum exfoliatum ssp. *suffruticans* (P.A.Duvign.) P.A.Duvign. & Bre (Figure 4h)	common	dwarf shrub	geoxylic grassland (ferralitic soils)	132754; 132825 (HBG)
Cryptosepalum maraviense Oliv. (Figure 4g)	common	dwarf shrub	geoxylic grassland (ferralitic soils)	135308B; 135620 (HBG)
Dalbergia nitidula Welw. ex Baker	rare	shrub / tree	woodland / forest	139236 (LUBA)
Dialium englerianum Henriq.	frequent	shrub / tree	woodland / forest	133147; 139034 (LUBA)
Dolichos sp. 140088	frequent	dwarf shrub / geoxyle	geoxylic grassland (ferralitic soils)	140088 (LUBA)
Entada arenaria Schinz	very rare	dwarf shrub	geoxylic grassland (sandy soils)	134147 (HBG)
Eriosema sp. 133109	rare	dwarf shrub	geoxylic grassland (ferralitic soils)	133109 (HBG)
Eriosema sp. 132895	rare	dwarf shrub	geoxylic grassland (ferralitic soils)	132753; 132895 (HBG)
Erythrina abyssinica Lam. ex DC.	very rare	tree	giant termite mounds	-
Erythrophleum africanum (Welw. ex Benth.) Harms	common	tree	woodland / forest	135333 (HBG)
Guibourtia coleosperma (Benth.) J.Léonard	occasional	tree	woodland / forest	139054 (LUBA)
Humularia welwitschii (Taub.) P.A.Duvign.	common	dwarf shrub	woodland / forest	139146 (LUBA)
Indigofera baumiana Harms	frequent	shrub	woodland / forest	132530 (HBG)
Indigofera congesta Welw. ex Baker	occasional	dwarf shrub	woodland / forest	139237 (LUBA)
Kotschya strobilantha (Welw. ex Baker) Dewit & P. A. Duvign. var. *strobilantha*	rare	dwarf shrub / geoxyle	geoxylic grassland (ferralitic soils)	139141 (LUBA)
Mucuna sp. 140052	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140052 (LUBA)
Pericopsis angolensis (Baker) Meeuwen	frequent	shrub / tree	woodland / forest	139181 (LUBA)
Pterocarpus angolensis DC	occasional	tree	woodland / forest	-

Continued

Table 1. *Continued.*

Species name	Frequency	Life form	Habitat	Collection number(s)
Hypericaceae				
Psorospermum febrifugum Spach.	rare	shrub / tree	woodland / forest	139036 (LUBA)
Psorospermum tenuifolium Hook.f.	rare	shrub / tree	woodland / forest	132958 (HBG)
Ixonanthaceae				
Phyllocosmus lemaireanus (De Wild. & T.Durand) T.Durand & H.Durand	common	shrub	woodland / forest	132968; 133005; 133149 (HBG)
Lamicaceae				
Alvesia rosmarinifolia Welw.	occasional	shrub	woodland / forest	134776; 132533 (HBG)
Tinnea sp. 133121	frequent	dwarf shrub	geoxylic grassland (ferralitic soils)	133121 (HBG)
Vitex doniana Sweet	occasional	shrub	woodland / woodland ecotone	132915 (HBG)
Vitex madiensis Oliv.	frequent	shrub	woodland / woodland ecotone	132996 (HBG); 139069 (LUBA)
Melastomataceae				
Memecylon flavovirens Baker	frequent	shrub / tree	woodland / forest	132519; 133161 (HBG); 139240 (LUBA)
Warneckea sapinii (De Wild.) Jacq.-Fél. (Figure 4d)	occasional	tree	woodland / forest	135309 (HBG); 139140 (LUBA)
Meliaceae				
Ekebergia benguelensis Welw. ex C.DC.	occasional	shrub	woodland / forest	132546; 133000; 133096 (HBG)
Moraceae				
Ficus pygmaea Welw. ex Hiern	rare	dwarf shrub	wetland margin	141510 (HBG)
Ficus sp. 141539	rare	dwarf shrub	Wetland margin	141539 (HBG)
Myricaceae				
Morella cf. *serrata* (Lam.) Killick	rare	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	140118 (LUBA)
Myrsinaceae				
Myrsine africana L.	common	shrub	woodland / forest	134107; 134278 (HBG); 139024 (LUBA)
Myrtaceae				
Syzygium guineense ssp. *barotsense* F.White	occasional	tree	woodland / forest	135813 (HBG)
Syzygium guineense ssp. *macrocarpum* (Engl.) F.White	common	shrub / tree	woodland ecotone	135800; 135796 (HBG)
Syzygium guineense ssp. *huillense* (Hiern) F.White	frequent	dwarf shrub	geoxylic grassland (sandy soils)	133072; 135614; 135882 (HBG)
Ochnaceae				
Ochna afzelii ssp. *mechowiana* R.Br. ex Oliv.	rare	dwarf shrub / geoxyle	woodland / grassland	133128 (HBG)
Ochna arenaria De Wild. & T.Durand (Figure 4e)	frequent	dwarf shrub	woodland, geoxylic grassland (sandy and ferralitic soils)	132947; 133024 (HBG); 140016 (LUBA)
Ochna manikensis De Wild.	frequent	dwarf shrub	geoxylic grassland (sandy soils)	132654; 132803 (HBG)
Ochna pulchra Hook.	common	shrub / tree	woodland / forest	135381; 139064 (LUBA)
Ochna pygmaea Hiern	common	dwarf shrub / geoxyle	woodland / forest, grassland (sandy soils)	139239; 140154 (LUBA)
Olacaceae				
Jasminum pauciflorum Benth.	rare	liana / shrub	woodland / forest	139238 (LUBA)
Schrebera trichoclada Welw.	rare	shrub / tree	woodland / forest	139189 (LUBA)
Orobanchaceae				
Sopubia karaguensis Oliv.	rare	dwarf shrub	woodland / forest	139033 (LUBA)
Passifloraceae				
Paropsia brazzaeana Baill.	common	shrub	woodland / forest	135299 (HBG); 139242 (LUBA)
Picodendraceae				
Oldfieldia dactylophylla (Welw. ex Oliv.) J.Léonard	rare	shrub / tree	woodland / forest	139208 (LUBA)
Polygalaceae				
Securidaca longepedunculata Fresen	occasional	tree	woodland / forest	133017 (HBG)
Polygonaceae				
Oxygonum fruticosum Dammer ex Milne-Redh.	frequent	shrub	woodland / forest	135322; 133032 (HBG); 139164 (LUBA)
Proteaceae				
Faurea intermedia Engl. & Gilg	occasional	shrub / tree	woodland / forest	132720; 139072 (LUBA)
Faurea rochetiana (A.Rich.) Chiov. ex Pic.Serm.	frequent	tree	woodland / forest / ecotone	135307 (HBG)
Faurea saligna Harv.	occasional	tree	geoxylic grassland (ferralitic soils)	132549; 132980; 134205 (HBG)
Protea baumii Engl. &Gilg.	occasional	dwarf shrub	woodland / forest	132501; 133019; 134225 (HBG)
Protea gaguedi J.F.Gmel.	frequent	tree	woodland / forest	132918 (LUBA)
Protea angolensis var. *divaricarta* (Engl. & Gilg.) Beard	rare	dwarf shrub	geoxylic grassland (ferralitic soils)	134200 (HBG)
Protea micans ssp. *trichophylla* Welw.	occasional	dwarf shrub	geoxylic grassland (sandy soils)	132607 (HBG); 140096 (LUBA)

Proteaceae, *continued*

Continued

Table 1. *Continued.*

Species name	Frequency	Life form	Habitat	Collection number(s)
Protea petiolaris ssp. *petiolaris* (Hier) Baker & C.H.Wright	frequent	tree	woodland / forest	132982 (HBG)
Protea cf. *welwitschii* Engl.	rare	dwarf shrub	geoxylic grassland (ferraliticsoils)	132480 (HBG)
Protea sp. 133045	rare	dwarf shrub	geoxylic grassland (sandy soils)	133045 (HBG)
Rhamnaceae				
Ziziphus mucronata Willd.	rare	shrub	woodland / forest	133093; 135285 (HBG)
Rubiaceae				
Ancylanthos rubiginosus Desf.	rare	dwarf shrub	geoxylic grassland (on sandy soils) & woodland ecotone	136003 (HBG)
Fadogia cf. *chrysantha* K.Schum.	very rare	shrub	woodland ecotone	134257 (HBG)
Fadogia cf. *triphylla* var. *triphylla* Baker	very rare	shrub	woodland / forest	132987 (HBG); 133081 (HBG)
Fadogia fuchsioides Welw. ex Oliv. (Figure 4c)	occasional	shrub	woodland / forest	132524 (HBG)
Fadogia cf. *homblei* De Wild.	rare	dwarf shrub / geoxyle	geoxylic grassland	140114 (LUBA)
Fadogia cf. *monticola* Robyns	rare	dwarf shrub / geoxyle	geoxylic grassland	140146 (LUBA)
Fadogia sp. 134097	occasional	shrub	geoxylic grassland (ferralitic soils), woodland ecotone	132453; 134097; 134167 (HBG)
Gardenia brachythamnus (K.Schum.) Launert	very rare	dwarf shrub	woodland ecotone	135338 (HBG)
Keetia cf. *gracilis* (Hiern) Bridson	very rare	shrub	woodland / forest	132442; 133148 (HBG)
Keetia venosa (Oliv.) Bridson	rare	shrub	woodland / forest	132534A (HBG)
Leptactina benguellensis (Welw. ex Benth. & Hook.f.) R.D.Good	rare	dwarf shrub	woodland / forest	135313; 135353; 133153 (HBG)
Leptactina prostrata K.Schum	very rare	dwarf shrub	geoxylic grassland (ferralitic soils)	134181 (HBG)
Pachystigma pygmaeum (Schltr.) Robyns	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140138 (LUBA)
Pygmaeothamnus cf. *chamaedendrum* (Kuntze) Robyns	very rare	dwarf shrub	geoxylic grassland (sandy soils)	132723 (HBG)
Pygmaeothamnus sp. 132552	very rare	dwarf shrub	woodland / forest	132552 (HBG)
Pygmaeothamnus zeyheri (Sond.) Robyns	rare	dwarf shrub	geoxylic grassland (sandy soils)	132798; 133033; 134089 (HBG)
Rytigynia orbicularis (K.Schum.) Robyns	frequent	shrub	woodland / forest	132925; 134127 (HBG); 139056 (LUBA)
Tapiphyllum cf. *psammophilum* (S.Moore) Robyns	very rare	shrub	woodland / forest	134279 (HBG)
Tricalysia angolensis A.Rich. ex DC.	very rare	shrub	woodland / forest	132500; 133012 (HBG)
Tricalysia sp. 134221	rare	shrub	woodland / forest	134221 (HBG)
Tricalysia coriacea ssp. *nyassae* (Benth.) Hiern	occasional	shrub	woodland / forest	133008; 134095; 134170 (HBG)
Tricalysia sp. 135367	very rare	shrub	woodland / forest	135367 (HBG)
Santalaceae				
Thesium sp. 139228	rare	dwarf shrub	woodland / forest	139228 (LUBA)
Sapotaceae				
Chrysophyllum bangweolense R.E.Fr.	rare	tree	woodland / forest	135359 (HBG)
Englerophytum magalismontanum (Sond.) T.D.Penn.	common	shrub	woodland / forest	135320 (HBG); 133151 (HBG); 139109 (LUBA)
Smilacaceae				
Smilax anceps Willd.	rare	shrub	woodland / forest	135308A (HBG)
Strychnaceae				
Strychnos cocculoides Baker	frequent	shrub / tree	woodland / forest	139070 (LUBA)
Strychnos pungens Soler.	common	shrub / tree	woodland / forest	139254 (LUBA)
Strychnos spinosa Lam.	occasional	tree	woodland / forest	135301 (HBG)

field work for this study (Gonçalves et al. 2016). In the case of *Combretum schumannii* Engl. literature indicated that the range of the species might extend to Angola (Exell & Wild 1960). However, neither this taxon nor its synonyms were included in the Angolan checklist (Figueiredo & Smith 2008).

Most of the species occurred either in the geoxylic grasslands or in the woodlands and forests. However, many of the geoxylic suffrutices have closely related tree species growing nearby in the woodlands (Figures 4h and 4i). In Africa, the centre of diversity of geoxylic suffrutices is in the Zambezian phytoregion. In regions with similar environmental conditions, such as the Sudanian phytoregion, there is only a very limited number of geoxylic species (White 1976).

We found two types of geoxylic grasslands, each harbouring a very distinct species pool with only a small overlap. There is much debate on the environmental factors driving the emergence of this distinct life form (Davy 1922; White 1976; Maurin et al. 2014; Finckh et al. 2016). However, the different species composition of the two types of geoxylic grasslands found in Cusseque can be clearly attributed to the contrasting edaphic conditions. The two dominant species in the "geoxylic grasslands on ferralitic soils" *Cryptosepalum maraviense* (Figure 4g) and *C. exfoliatum* ssp. *suffruticans*

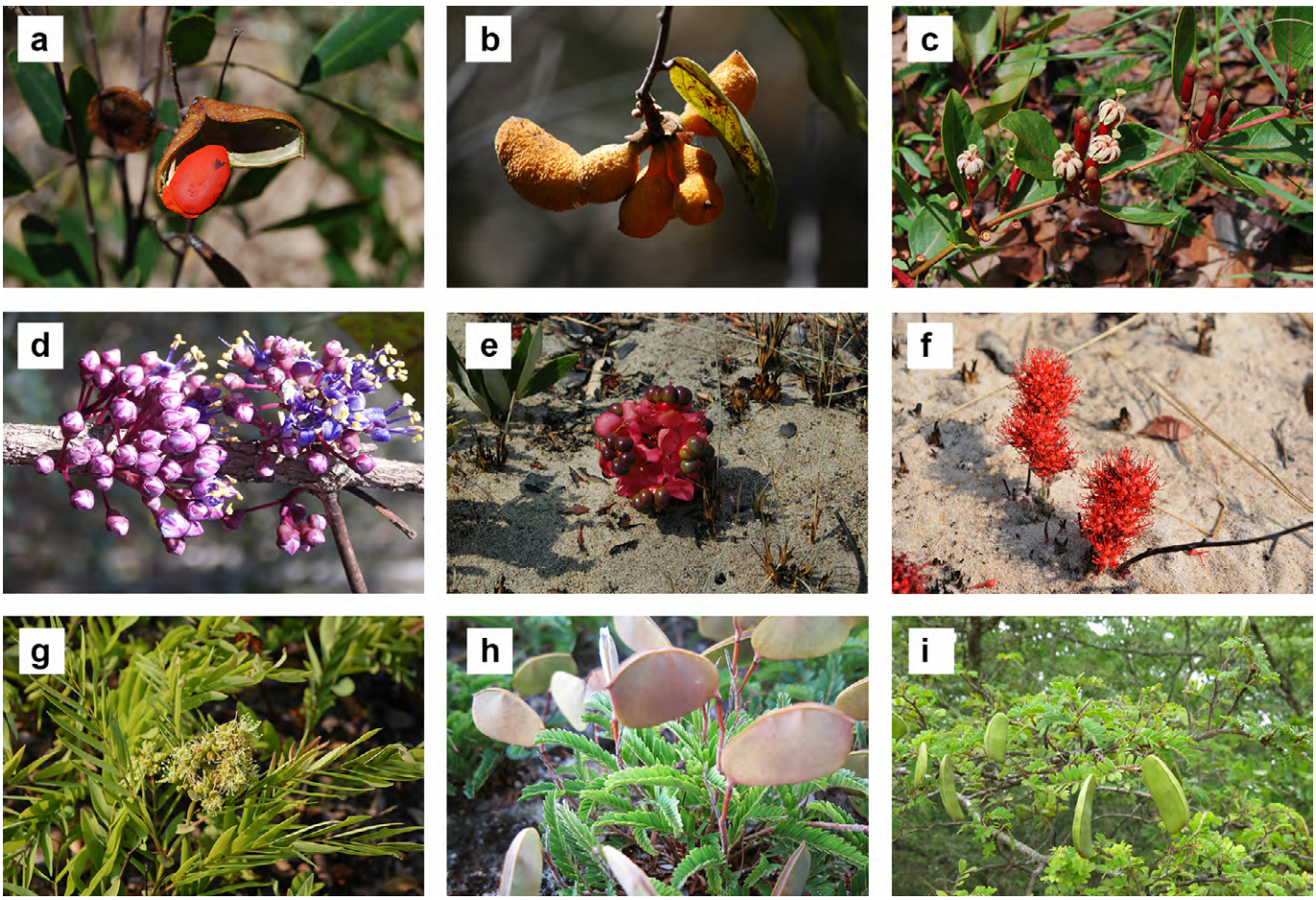

Figure 4 Typical plants of the Cusseque area: **a)** *Copaifera baumiana*, **b)** *Uvaria angolensis*, **c)** *Fadogia fuchsioides*, **d)** *Warneckea sapinii*, **e)** *Ochna arenaria*, **f)** *Combretum platypetalum* ssp. *platypetalum*, **g)** *Cryptosepalum maraviense*, **h)** *Cryptoseplaum exfoliatum* ssp. *suffruticans*, **i)** *Cryptosepalum exfoliatum* ssp. *pseudotaxus*.

(Figure 4i) belong to the Fabaceae. In contrast, the "geoxylic grasslands on sandy soils" were dominated by various species of the genus *Ochna* of the Ochnaceae and *Parinari capensis* of the Chrysobalanaceae. The "geoxylic grasslands on ferralitic soils" have their core distribution on the Angolan Central Plateau and make up 8.5% of the land surface within the Cubango Basin (Revermann et al. in revision). The "geoxylic grasslands on sandy soils" have a very limited distribution within the study site and cover 0.7% of the area of the Cubango Basin. However, they are more extensive further east in the Cuito River Basin and in eastern Moxico Province, where they occur on large sandy, alluvial plains of the Zambezi Graben, e.g., in Cameia National Park.

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LISTS OF SPECIES

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Woody species of the Miombo woodlands and geoxylic grasslands of the Cusseque area, south-central Angola

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Abstract: The species composition of the vegetation in most regions of Angola has been poorly studied and most studies date back to the pre-independence era. In this study, we provide a detailed account of the woody flora of the Miombo woodlands and geoxylic grasslands of the Cusseque study site of "The Future Okavango" (TFO) project, situated on the Angolan Central Plateau. The checklist is based on a vegetation survey using vegetation plots of 1,000 m^2 and also includes records from botanical collections made elsewhere at the study site. In total, we documented 154 woody species belonging to 99 genera of 37 plant families in 100 km^2. The study represents the first comprehensive account of the woody vegetation of the area including all habitats and growth forms.

Key words: Angola; Bié; geoxylic suffrutex; Miombo; The Future Okavango project; vegetation survey

INTRODUCTION

Rural communities in Angola hold an enormous knowledge of the local flora and especially have great understanding of the potential usages of plants (Figueiredo & Smith 2012; Kissanga 2016). In contrast, scientific exploration and documentation of the vegetation of Angola is still limited. Early botanists such as Friedrich Welwitsch visited the country in the middle of the 19th century (Welwitsch 1869). The most influential botanist working in Angola in the first half of the 20th century was John Gossweiler, who worked in all Angolan provinces and collected over 14,000 specimens. His collection is considered an especially important source of information for rare and endemic species (Figueiredo & Smith 2008). Furthermore, Gossweiler produced the first phytogeographic map of Angola containing 19 principal vegetation types (Gossweiler & Mendonça 1939). Based on this map and his own observations, Luís A. Grandvaux Barbosa published a new phytogeographic map in 1971 containing 32 main types and over 100 subordinate types dealt with in the text (Barbosa 1970, 1971). However, the descriptions of these vegetation types were of general character and limited to the dominant species. Detailed descriptions of the species composition and plant diversity of the Angolan vegetation are lacking for most parts of the country. For the province of Bié, Monteiro (1970) provided an excellent overview on the woody vegetation including the first provincial map of the woodlands. Based on 144 relevés, Monteiro delineated three associations of woody plants and four sub-associations.

The civil war that followed Angola's independence in 1975 made any scientific work in Angola extremely difficult, and thus, most scientific literature available today dates back to the pre-independence era. Since the end of the armed conflict in 2002, scientific work is slowly increasing. However, botanical work in the country is still hampered by the lack of field guides and the fact that the principal work on the flora of Angola, the *Conspectus Florae Angolensis,* remains unfinished and important families such as the Rubiaceae are not treated. Similarly, a countrywide checklist of the flora of Angola was lacking until the recent publication of "Plants of Angola – Plantas de Angola" by Figueiredo & Smith (2008). Nevertheless, inventories of vascular plants at the local and regional scale are still lacking for most parts of the country. Such inventories are indispensable for any kind of natural resource management planning, conservation measures or ecological studies (Figueiredo et al. 2009).

The interdisciplinary research project "The Future Okavango" (TFO) aims to provide a scientific basis for strategic resource planning for the Okavango Basin. The headwaters of the Okavango River, where 95% of the runoff are generated, are located on the Angolan Central Plateau (Steudel et al. 2013). Rapid transformations of the social-ecological systems are currently taking place there (Pröpper et al. 2015). However, little knowledge

and data on the vegetation and the botanical diversity was available (Revermann 2016). In this study, we present results of the vegetation survey carried out at the research site "Cusseque" in the province of Bié located at the upper reaches of the Okavango River.

MATERIALS AND METHODS

Study site

The Okavango River originates on the Angolan Central Plateau and terminates in a large inland delta in the Kalahari Desert in Botswana. Within the TFO project, detailed studies were carried out at four research sites representing the different parts of the river basin. The work presented in this paper was carried out at the study site Cusseque with an area of 100 km^2 (13.6985° S, 017.0382° E). The site is located on the Angolan Central Plateau in the province of Bié (Figure 1; Wehberg & Weinzierl 2013). The landscape can be described as a rolling plain intersected by the Cusseque River and its many tributaries, which are orientated perpendicular to each other. Three major landscape units can be identified: the elevated areas, the sloping areas leading down to the valley bottoms and the valley floors (Gröngröft et al. 2013b). The mean elevation is 1,575 m above sea level while the difference in elevation between the valley bottom of the main river and the surrounding elevated areas is about 100 m (Gröngröft et al. 2013b). The climate of the Cusseque area is semi-humid with a pronounced wet season lasting from November to April. The mean annual precipitation is 987 mm and the mean annual temperature is 20.4°C (Weber 2013). The study area harbours a high pedodiversity. The elevated areas are characterized by deep and developed slightly loamy Arenosols. The slopes of the smaller valleys of the tributaries and at the western side of the Cusseque River show shallow Plinthisols on granitic bedrock. The soils along the eastern part of the Cusseque River are characterized by very deep and leached Arenosols. The centre of the valleys support Histosols with peat layers exceeding 1 m in depth while at the edges of the wetlands Gleysols are the common soil type (Gröngröft et al. 2013a).

The main vegetation types covering south central Angola are semi-deciduous Miombo woodlands and forests (Figures 2a and b). These woodlands are interspersed with open vegetation types locally termed *anharas de ongote*. The salient feature of the open vegetation types are dwarf shrubs with a huge underground woody biomass. This distinct life form was described by White (1976) as "geoxylic suffrutex". In the Cusseque area, geoxylic suffrutices occur on two different soil types: on deep, leached sandy soils and on shallow, compact, ferralitic soils. Accordingly, we will differentiate herein between "geoxylic grasslands on sandy soils" (Figure 2c) and "geoxylic grasslands on ferralitic soils" (Figure 2d). The occurrences of the different vegetation types are governed by topography: woodlands and forests are confined to the elevated areas and upper slopes. The mid- and lower

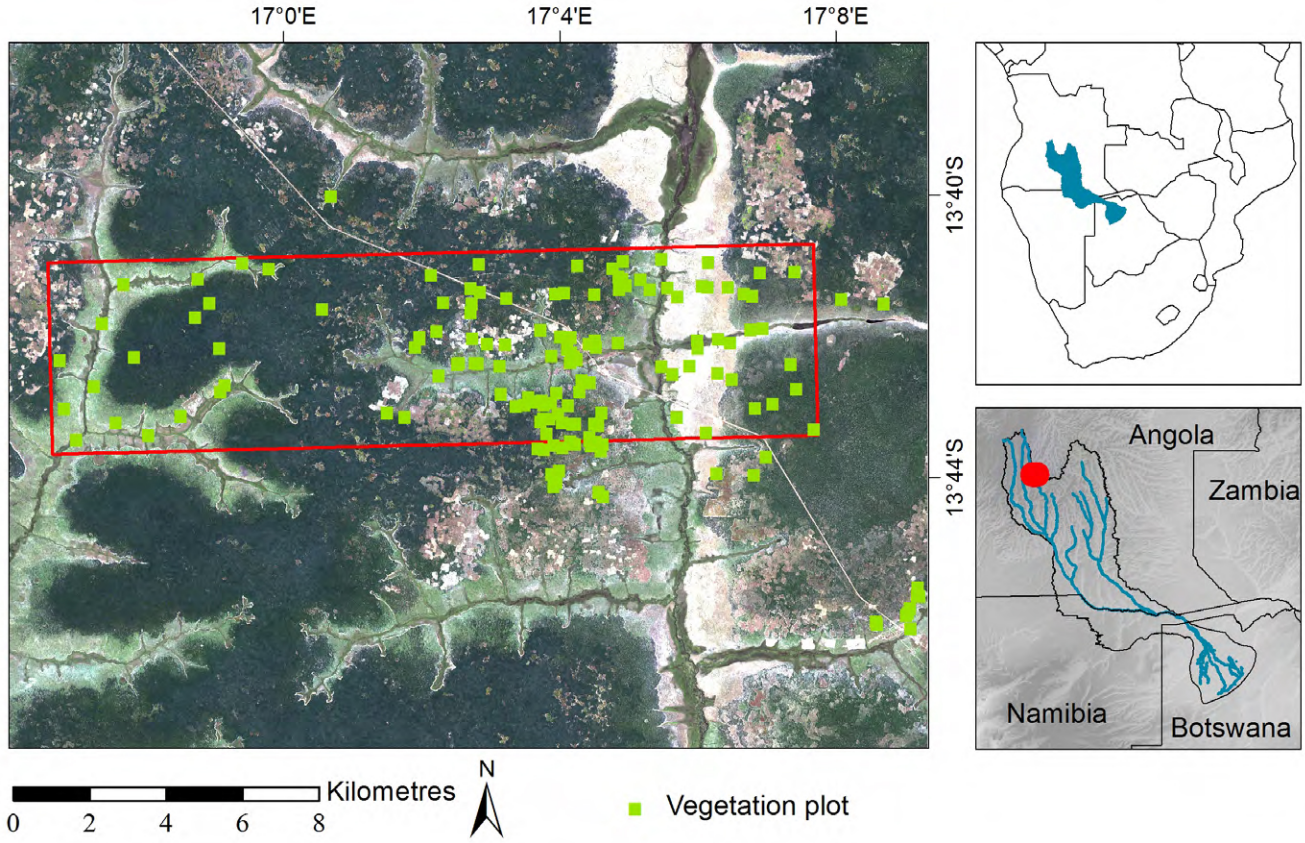

Figure 1. Location of the Okavango Basin in southern Africa and the study site "Cusseque" denoted in red. (Projection: WGS 1984; background: RapidEye high-resolution satellite imagery, recorded 1 May 2013. We acknowledge the DLR for the provision of the data from the RapidEye Science Archive.)

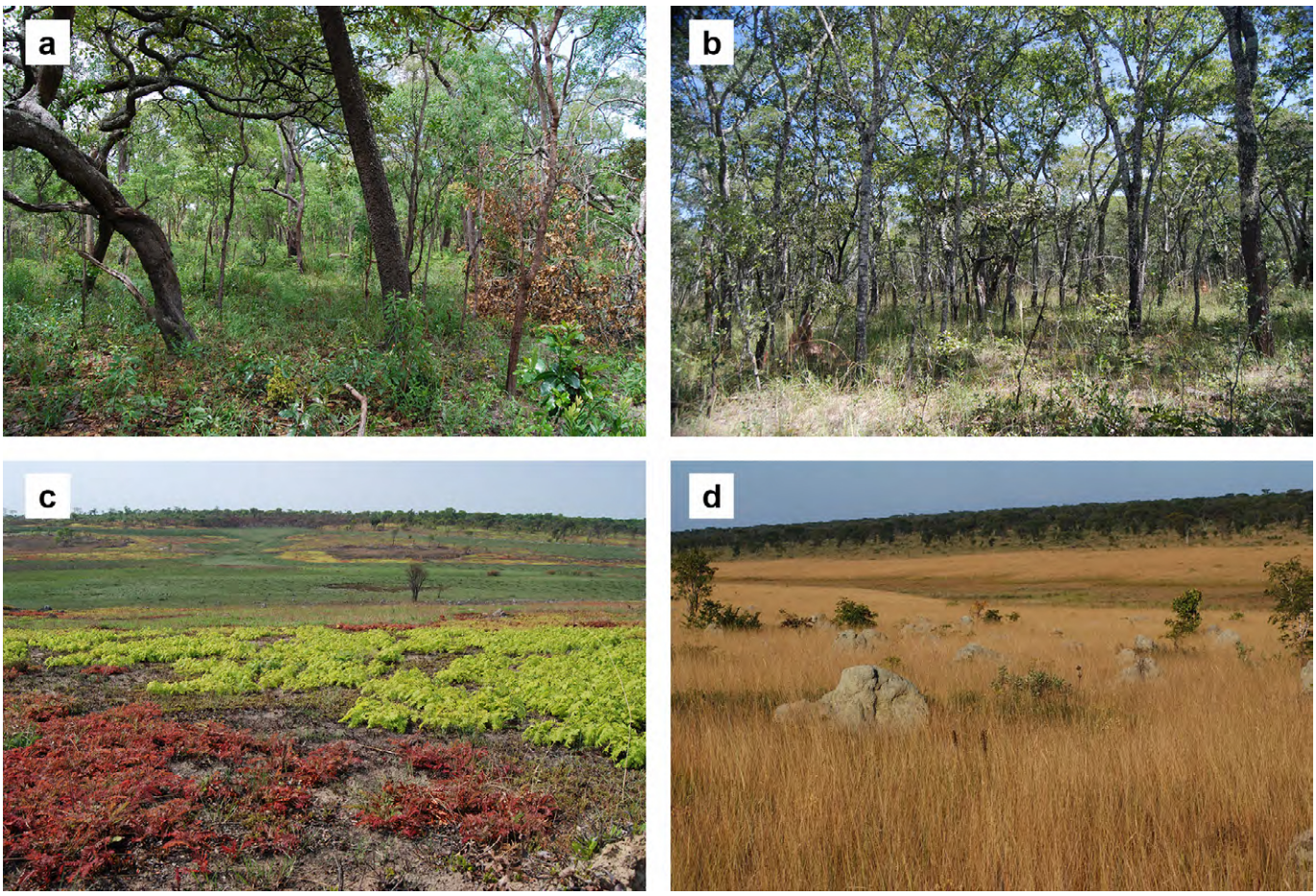

Figure 2. Landscapes of the Cusseque study area: **a)** Miombo woodland in the middle of the rainy season, **b)** Miombo woodland at the end of the rainy season, **c)** geoxylic grasslands dominated by *Cryptosepalum maraviense* at the beginning of the rainy season in October, **d)** geoxylic grassland on sandy soils at the beginning of the dry season in May; in the background wetland on the valley bottom and Miombo woodlands.

slopes feature geoxylic grasslands. The woodlands and geoxylic grasslands are separated by ecotones extending up to several hundred meters where elements of both vegetation types co-occur. The valley bottoms support wetlands dominated by Cyperaceae (Revermann et al. 2013; Schneibel et al. 2013).

Data collection

Plot based vegetation surveys were carried out during the growing season in the years 2011 to 2014 and all information is stored in the Vegetation Database of the Okavango Basin (GIVD ID: AF-00-009, Revermann et al. 2016). In order to evenly map all existing vegetation units, sampling followed a random, stratified design. Based on an image segmentation algorithm using all bands of a Landsat 7 scene, seven major vegetation units were identified. In these vegetation units random points were created using GIS and transferred to a hand-held GPS for localization in the field. Furthermore, additional vegetation plots were examined in different successional stages of Miombo forest to analyse successional pathways of the regeneration of natural vegetation after disturbance by shifting cultivation (Gonçalves et al., accepted). We used a nested plot design with a 10 m × 10 m plot located in the centre of a 20 m × 50 m plot. In total, we sampled 148 vegetation plots. Due to the unique character of the geoxylic grasslands, these were subject to an additional field study. Therein, data were collected using 10 m × 10 m plots with two 3.3 m × 3.3 m subplots situated in diagonally opposite corners (adapted from Dengler 2009). In every plot all vascular plants found were recorded and their projected cover estimated visually. Unknown plants were photographed and voucher specimens were collected according to botanical methods outlined by Victor et al. (2004). Voucher specimens were deposited in the herbarium of the ISCED Huíla (LUBA) and in the Herbarium Hamburgense (HBG). In addition to the species recorded on the vegetation plots, species found elsewhere while working at the study area were added to the checklist. A high number of vegetation plots and several months of field work carried out by four observers in all seasons ensured a comprehensive coverage of the woody species present at the study area.

Taxonomy and plant identification

We followed the taxonomy of the checklist "Plants of Angola – Plantas de Angola" by Figueiredo & Smith (2008). We are aware of recent changes in the taxonomy, but decided to conform to the national checklist. For identification, we consulted the *Conspectus Florae Angolensis* (Exell & Mendonça 1937, 1951, 1954, 1955; Exell & Fernandes

1962, 1966; Exell et al. 1970) when possible, and the flora of neighbouring countries, especially the *Flora Zambeziaca* (Exell & Wild 1960) and the field guide to the *Trees and shrubs of Namibia* (Mannheimer & Curtis 2009). Additionally, we consulted herbarium collections at the ISCED Huíla (LUBA) and the Instituto de Investigação Científica Tropical (LISC) as well as the on-line database JSTOR Plant Science (http://plants.jstor.org/). For some specimens, we consulted experts at Kew Botanical Garden (K).

Permits

Permits for plant collection and transfer of biological material in Angola for scientific purposes was arranged based on the framework of Material Transfer Agreements from Angola, negotiated between the Instituto Superior de Ciências de Educação da Huíla (ISCED, Huíla), Lubango and the University of Hamburg (UHH), Germany and authorized on behalf of the Angolan Government by the Director for Agriculture, Fisheries and Environment of the Province of Huíla. All International Conventions to which Angola is signatory country, such as Convention on International Trade in Endangered Species of Wild Fauna and Flora (1973), Convention on Biological Diversity (1992), International Treaty on Plant Genetic Resources for Food and Agriculture (2004), and all other relevant national and international instruments concerning biodiversity were taken into account.

Data analysis

We visualized the number of species per family of all species belonging to one family using the function 'pie' in the statistical software R (R Development Core Team 2016). Data on the frequency of occurrence of a species, the habitat and the life form were compiled from vegetation plot data. We assigned frequency according to the following categories: very rare (1 or 2 observations), rare (3–5 observations), occasional (6–10 observations), frequent (11–30 observations), common (>30 observations). We assigned every species to one or more of the following life form categories based on field observations and literature: tree, shrub, liana, dwarf shrub and geoxyle. For geoxyles we followed the definition proposed by White (1976). White defined a geoxyle as a dwarf shrub that has closely related species growing as trees and that exhibits massive woody underground parts.

RESULTS

We documented 154 woody species belonging to 99 genera and 37 families (Table 1). The majority of species belonged to the family Fabaceae (33), followed by Rubiaceae (22), Euphorbiaceae (11), Proteaceae (10) and Combretaceae (9) (Figure 3). Most of the dominant species belonged to the Fabaceae and occurred with high frequencies. In contrast, the Rubiaceae, second in species richness, contained species occurring with low frequencies and were less abundant. The woodlands and forests showed the highest woody species richness with 110 species belonging to 32 families. A surprisingly high number of 33 woody species from 14 families were found in the geoxylic grasslands. These open vegetation types appear to be merely grasslands in the late growing season (Figures 2c and d) but in fact harbour a remarkable diversity of woody species (Table 1). In the wetlands few woody species occurred and we recorded only two *Ficus* species sporadically occurring along the margins of the wetlands.

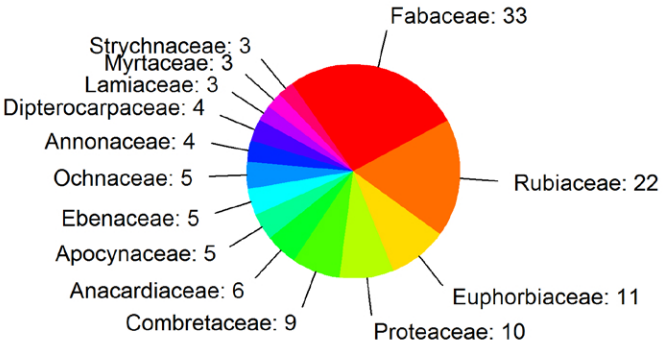

Figure 3. The families of woody plants found at the Cusseque study site, south-central Angola. Only families with more than two species are shown. In total 37 families of woody plant species occurred, containing 154 species in 99 genera.

One species, *Combretum schumannii* Engl., was recorded but is not listed in the current checklist of Angola (Figueiredo & Smith 2008).

DISCUSSION

The 154 species recorded within the 100 km^2 of the Cusseque study site almost equalled the 166 woody species found by Monteiro (1970) in the entire province of Bié, an area of 70,314 km^2. This does not reflect the quality of the study of Monteiro but rather illustrates how poorly the region has been surveyed so far. In fact, the study carried out by Monteiro (1970) is of high quality and stands out as the only study of its time from Angola basing its analysis on quantitative, plot based data. However, the study was restricted to woodlands and only larger shrubs and trees were included. In contrast, we included all vegetation types ranging from woodlands to geoxylic grasslands and wetlands. Due to the high sampling intensity and the coverage of all vegetation types our species list can therefore be considered a comprehensive checklist of the woody plant species of the Cusseque area. However, it must be noted that this list does not contain any specimen that could not be identified to at least genus level; some specimens were lacking fruits or flowers, preventing further identification. Therefore, the actual number of woody species may be slightly higher.

Despite the relatively recent publication of the checklist of vascular plants of Angola, subsequent field surveys in various parts of the country have resulted in additions to the checklist (Huntley & Coelho 2011). We provided the first record in Angola of the herbaceous Asteraceae *Schistostephium crataegifolium* (DC.) Fenzl ex Harv, during the

Table 1. List of species arranged by family. Voucher specimens have been deposited in the herbaria of Lubango (LUBA) and Hamburg (HBG). In most cases doublets are stored in both herbaria. The herbarium name in parentheses is the location where the specimen used for identification is deposited. Frequency was assigned according to the following categories: very rare (1 or 2 observations), rare (3–5 observations), occasional (6–10 observations), frequent (11–30 observations), common (>30 observations). Life forms of the species were assigned to one or more of the categories: tree, shrub, liana, dwarf shrub and geoxyle.

Species name	Frequency	Life form	Habitat	Collection number(s)
Anacardiaceae				
Ozoroa cf. xylophylla (Engl. &Gilg) R.Fern. & A.Fern.	very rare	shrub	geoxylic grassland (sandy soils)	133057B (HBG)
Ozoroa stenophylla Engl. & Gilg.	frequent	shrub	woodland / grassland (ferralitic soils)	140123 (LUBA)
Rhus arenaria Torre, A.R.	frequent	dwarf shrub / geoxyle	geoxylic grassland (ferralitic soils)	140101 (LUBA)
Rhus exelliana Meikle	frequent	dwarf shrub		135250; 134275 (HBG)
Rhus gracilipes Exell	frequent	dwarf shrub	woodland / forest	139227; 132483 (HBG)
Rhus kirkii Oliv.	frequent	dwarf shrub	woodland / forest	139253 (LUBA)
Anisophylleaceae				
Anisophyllea boehmii Engl.	frequent	tree	woodland / forest	134316; 139018; 135297 (HBG)
Anisophyllea quangensis Engl. ex Henriq.	rare	dwarf shrub	geoxylic grassland (sandy soils)	133044; 134116 (HBG); 140109 (LUBA)
Annoncaceae				
Annona stenophylla ssp. *nana* Engl. & Diels	rare	dwarf shrub	woodland / forest	133058; 134218 (HBG); 140065 (LUBA)
Uvaria angolensis Welw. ex Oliv. (Figure 4b)	frequent	shrub	woodland / forest	135323; 134240 (HBG)
Xylopia odoratissima Welw. ex Oiv.	frequent	shrub	woodland / forest	133057A; 134263 (HBG)
Xylopia tomentosa Exell	common	shrub	woodland / forest	135279; 132956; 132986 (HBG); 139177 (LUBA)
Apocynaceae				
Chamaeclitandra henriquesiana (Hallier f.) Pichon	common	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140121 (LUBA)
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	frequent	shrub / tree	woodland / forest	135300 (HBG)
Landolphia camptoloba (K.Schum.) Pichon	frequent	liana	woodland / forest	132537 (HBG)
Landolphia gossweileri (Stapf) Pichon	rare	dwarf shrub	geoxylic grassland (sandy soils)	133048 (HBG)
Strophanthus welwitschii (Baill.) K.Schum.	frequent	liana	woodland / forest	135336; 135378; 134091 (HBG)
Asparagaceae				
Asparagus sp. 135286	frequent	shrub	woodland / forest	135286 (HBG)
Asparagus cf. *africanus* Lam.	very rare	shrub	woodland / forest	134115 (HBG)
Asteraceae				
Helichrysum krausii Sch. Bip	occasional	shrub	woodland / forest	132695 (HBG)
Crysobalanaceae				
Parinari capensis Harv.	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	132664; 132898; 140068 (HBG)
Parinari curatellifolia Planch. ex Benth.	common	tree	woodland / forest	132444 (HBG)
Combretaceae				
Combretum acutifolium Exell	very rare	liana / shrub	woodland / forest	135306 (HBG)
Combretum collinum Fresen.	common	tree	woodland / forest	139176 (HBG)
Combretum elaeagnoides Klotzsch	very rare	tree	woodland / forest	132538 (HBG)
Combretum engleri Schinz	frequent	shrub	woodland / forest	133216 (HBG)
Combretum platypetalum ssp. *platypetalum* Welw. ex M.A.Lawson (Figure 4f)	occasional	dwarf shrub	geoxylic grassland (sandy soils)	132639; 134114; 140113 (HBG)
Combretum schumannii Engl.	rare	shrub	woodland / forest	139048 (LUBA)
Combretum zeyheri Sond.	frequent	shrub / tree	woodland / forest	135280; 132510 (HBG)
Pteleopsis anisoptera (Welw.) Engl. & Diels	frequent	shrub / tree	woodland / forest	135365; 134110 (HBG); 139066 (LUBA)
Terminalia brachystemma Welw. ex Hiern	frequent	tree	woodland / forest / grassland (sandy and ferralitic soils)	132997; 134088; 134131 (HBG)
Dichapetalaceae				
Dichapetalum cymosum (Hook.) Engl.	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140165 (LUBA)
Dipterocarpaceae				
Monotes africanus A.DC.	common	tree	woodland / forest	132917; 134160; 134228 (HBG)
Monotes angolensis de Wild.	very rare	tree	woodland / forest	132443 (HBG)
Monotes caloneurus Gilg.	rare	tree	woodland / forest	134820 (HBG)
Monotes dasyanthus Gilg	common	tree	woodland / forest	132907; 132961 (HBG); 139228 (LUBA)
Ebenaceae				
Diospyros batocana Hiern	occasional	shrub / tree	woodland / forest	139247 (LUBA)
Diospyros chamaethamnus Dinter ex Mildbr.	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140179 (LUBA)

Continued

Table 1. *Continued.*

Species name	Frequency	Life form	Habitat	Collection number(s)
Ebenaceae, *continued*				
Diospyros pseudomespilus ssp. *brevicalyx* Mildbr.	frequent	shrub	woodland / forest	135379 (HBG)
Diospyros virgata (Gürke) Brenan	occasional	shrub	woodland / forest	132941 (HBG)
Euclea crispa ssp. *crispa* (Thunb.) Gürke	frequent	dwarf shrub	woodland / forest / geoxylic grassland	135413 (HBG)
Ericaceae				
Erica benguellensis (Welw. ex Engl.) E.G.H. Oliv.	very rare	shrub / tree	woodland / forest	139235 (LUBA)
Euphorbiaceae				
Bridelia sp. 139095	occasional	shrub / tree	woodland / forest	139095 (LUBA)
Hymenocardia acida Tul.	frequent	shrub / tree	woodland / forest	134099; 134135 (HBG); 139068 (LUBA)
Maprounea africana Müll. Arg.	rare	shrub / tree	woodland / forest	139113 (LUBA)
Phyllanthus angolensis Müll. Arg.	rare	dwarf shrub	woodland / forest	139256 (LUBA)
Phyllanthus sp. 139238	common	dwarf shrub	woodland / forest	139238 (LUBA)
Phyllanthus welwitschianus Müll. Arg.	common	dwarf shrub	woodland / forest	139237 (LUBA)
Pseudolachnostylis maprouneifolia Pax	occasional	tree	woodland / forest	132555; 134232 (HBG); 139038 (LUBA)
Sclerocroton oblongifolius (Müll. Arg.) Kruijt & Roebers	frequent	dwarf shrub	woodland / forest	132990; 134185 (HBG)
Uapaca sp. 134199	common	dwarf shrub / geoxyle	geoxylic grassland (ferralitic soils)	132490; 134199 (HBG)
Uapaca kirkiana Müll. Arg.	common	tree	woodland / forest	-
Uapaca nitida var. *nitida* Müll. Arg.	common	tree	woodland / forest	132691; 132912; 132998 (HBG)
Fabaceae				
Abrus melanospermus ssp. *suffruticosus* (Boutique) D.K.Harder	occasional	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140167 (LUBA)
Albizia antunesiana Harms	frequent	tree	woodland / forest	134156; 135318 (HBG); 139223 (LUBA)
Albizia gummifera (J.F.Gmel) C.A.Sm.	occasional	shrub / tree	woodland / forest	139065; 135342; 132967 (HBG)
Baphia bequaertii De Wild.	frequent	shrub / tree	woodland / forest	135360; 139242; 133018 (HBG)
Bauhinia petersiana Bolle	common	shrub	woodland / forest	135311 (HBG)
Bobgunnia madagascariensis (Desv.) J.H.Kirkbr. & Wiersema	frequent	shrub / tree	woodland / forest	132963; 139128 (LUBA)
Brachystegia bakeriana Hutch. & Burtt Davy	common	tree	woodland / forest	135298; 139016 (LUBA)
Brachystegia longifolia Benth.	occasional	tree	woodland / forest	132957; 139255 (LUBA)
Brachystegia spiciformis Benth.	common	tree	woodland / forest	132676 (HBG)
Burkea africana Hook.	common	tree	woodland / forest	-
Copaifera baumiana Harms	common	shrub	woodland / forest	132900; 135335 (HBG); 139233 (LUBA)
Crotalaria amoena Welw. ex Baker	rare	dwarf shrub	woodland / forest	139121 (LUBA)
Crotalaria cistoides Welw. ex Baker	rare	dwarf shrub	woodland / forest	139257 (LUBA)
Crotalaria florida Welw. ex Baker	rare	dwarf shrub	woodland / forest	139196 (LUBA)
Cryptosepalum exfoliatum ssp. *pseudotaxus* (Baker f.) P.A.Duvign. & Brenan (Figure 4i)	common	tree	woodland / forest	135304 (HBG); 139023 (LUBA)
Cryptosepalum exfoliatum ssp. *suffruticans* (P.A.Duvign.) P.A.Duvign. & Bre (Figure 4h)	common	dwarf shrub	geoxylic grassland (ferralitic soils)	132754; 132825 (HBG)
Cryptosepalum maraviense Oliv. (Figure 4g)	common	dwarf shrub	geoxylic grassland (ferralitic soils)	135308B; 135620 (HBG)
Dalbergia nitidula Welw. ex Baker	rare	shrub / tree	woodland / forest	139236 (LUBA)
Dialium englerianum Henriq.	frequent	shrub / tree	woodland / forest	133147; 139034 (LUBA)
Dolichos sp. 140088	frequent	dwarf shrub / geoxyle	geoxylic grassland (ferralitic soils)	140088 (LUBA)
Entada arenaria Schinz	very rare	dwarf shrub	geoxylic grassland (sandy soils)	134147 (HBG)
Eriosema sp. 133109	rare	dwarf shrub	geoxylic grassland (ferralitic soils)	133109 (HBG)
Eriosema sp. 132895	rare	dwarf shrub	geoxylic grassland (ferralitic soils)	132753; 132895 (HBG)
Erythrina abyssinica Lam. ex DC.	very rare	tree	giant termite mounds	-
Erythrophleum africanum (Welw. ex Benth.) Harms	common	tree	woodland / forest	135333 (HBG)
Guibourtia coleosperma (Benth.) J.Léonard	occasional	tree	woodland / forest	139054 (LUBA)
Humularia welwitschii (Taub.) P.A.Duvign.	common	dwarf shrub	woodland / forest	139146 (LUBA)
Indigofera baumiana Harms	frequent	shrub	woodland / forest	132530 (HBG)
Indigofera congesta Welw. ex Baker	occasional	dwarf shrub	woodland / forest	139237 (LUBA)
Kotschya strobilantha (Welw. ex Baker) Dewit & P. A. Duvign. var. *strobilantha*	rare	dwarf shrub / geoxyle	geoxylic grassland (ferralitic soils)	139141 (LUBA)
Mucuna sp. 140052	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140052 (LUBA)
Pericopsis angolensis (Baker) Meeuwen	frequent	shrub / tree	woodland / forest	139181 (LUBA)
Pterocarpus angolensis DC	occasional	tree	woodland / forest	-

Continued

Table 1. *Continued.*

Species name	Frequency	Life form	Habitat	Collection number(s)
Hypericaceae				
Psorospermum febrifugum Spach.	rare	shrub / tree	woodland / forest	139036 (LUBA)
Psorospermum tenuifolium Hook.f.	rare	shrub / tree	woodland / forest	132958 (HBG)
Ixonanthaceae				
Phyllocosmus lemaireanus (De Wild. & T.Durand) T.Durand & H.Durand	common	shrub	woodland / forest	132968; 133005; 133149 (HBG)
Lamicaceae				
Alvesia rosmarinifolia Welw.	occasional	shrub	woodland / forest	134776; 132533 (HBG)
Tinnea sp. 133121	frequent	dwarf shrub	geoxylic grassland (ferralitic soils)	133121 (HBG)
Vitex doniana Sweet	occasional	shrub	woodland / woodland ecotone	132915 (HBG)
Vitex madiensis Oliv.	frequent	shrub	woodland / woodland ecotone	132996 (HBG); 139069 (LUBA)
Melastomataceae				
Memecylon flavovirens Baker	frequent	shrub / tree	woodland / forest	132519; 133161 (HBG); 139240 (LUBA)
Warneckea sapinii (De Wild.) Jacq.-Fél. (Figure 4d)	occasional	tree	woodland / forest	135309 (HBG); 139140 (LUBA)
Meliaceae				
Ekebergia benguelensis Welw. ex C.DC.	occasional	shrub	woodland / forest	132546; 133000; 133096 (HBG)
Moraceae				
Ficus pygmaea Welw. ex Hiern	rare	dwarf shrub	wetland margin	141510 (HBG)
Ficus sp. 141539	rare	dwarf shrub	Wetland margin	141539 (HBG)
Myricaceae				
Morella cf. *serrata* (Lam.) Killick	rare	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	140118 (LUBA)
Myrsinaceae				
Myrsine africana L.	common	shrub	woodland / forest	134107; 134278 (HBG); 139024 (LUBA)
Myrtaceae				
Syzygium guineense ssp. *barotsense* F.White	occasional	tree	woodland / forest	135813 (HBG)
Syzygium guineense ssp. *macrocarpum* (Engl.) F.White	common	shrub / tree	woodland ecotone	135800; 135796 (HBG)
Syzygium guineense ssp. *huillense* (Hiern) F.White	frequent	dwarf shrub	geoxylic grassland (sandy soils)	133072; 135614; 135882 (HBG)
Ochnaceae				
Ochna afzelii ssp. *mechowiana* R.Br. ex Oliv.	rare	dwarf shrub / geoxyle	woodland / grassland	133128 (HBG)
Ochna arenaria De Wild. & T.Durand (Figure 4e)	frequent	dwarf shrub	woodland, geoxylic grassland (sandy and ferralitic soils)	132947; 133024 (HBG); 140016 (LUBA)
Ochna manikensis De Wild.	frequent	dwarf shrub	geoxylic grassland (sandy soils)	132654; 132803 (HBG)
Ochna pulchra Hook.	common	shrub / tree	woodland / forest	135381; 139064 (LUBA)
Ochna pygmaea Hiern	common	dwarf shrub / geoxyle	woodland / forest, grassland (sandy soils)	139239; 140154 (LUBA)
Olacaceae				
Jasminum pauciflorum Benth.	rare	liana / shrub	woodland / forest	139238 (LUBA)
Schrebera trichoclada Welw.	rare	shrub / tree	woodland / forest	139189 (LUBA)
Orobanchaceae				
Sopubia karaguensis Oliv.	rare	dwarf shrub	woodland / forest	139033 (LUBA)
Passifloraceae				
Paropsia brazzaeana Baill.	common	shrub	woodland / forest	135299 (HBG); 139242 (LUBA)
Picodendraceae				
Oldfieldia dactylophylla (Welw. ex Oliv.) J.Léonard	rare	shrub / tree	woodland / forest	139208 (LUBA)
Polygalaceae				
Securidaca longepedunculata Fresen	occasional	tree	woodland / forest	133017 (HBG)
Polygonaceae				
Oxygonum fruticosum Dammer ex Milne-Redh.	frequent	shrub	woodland / forest	135322; 133032 (HBG); 139164 (LUBA)
Proteaceae				
Faurea intermedia Engl. & Gilg	occasional	shrub / tree	woodland / forest	132720; 139072 (LUBA)
Faurea rochetiana (A.Rich.) Chiov. ex Pic.Serm.	frequent	tree	woodland / forest / ecotone	135307 (HBG)
Faurea saligna Harv.	occasional	tree	geoxylic grassland (ferralitic soils)	132549; 132980; 134205 (HBG)
Protea baumii Engl. &Gilg.	occasional	dwarf shrub	woodland / forest	132501; 133019; 134225 (HBG)
Protea gaguedi J.F.Gmel.	frequent	tree	woodland / forest	132918 (LUBA)
Protea angolensis var. *divaricarta* (Engl. & Gilg.) Beard	rare	dwarf shrub	geoxylic grassland (ferralitic soils)	134200 (HBG)
Protea micans ssp. *trichophylla* Welw.	occasional	dwarf shrub	geoxylic grassland (sandy soils)	132607 (HBG); 140096 (LUBA)

Proteaceae, *continued*

Continued

Table 1. *Continued.*

Species name	Frequency	Life form	Habitat	Collection number(s)
Protea petiolaris ssp. *petiolaris* (Hier) Baker & C.H.Wright	frequent	tree	woodland / forest	132982 (HBG)
Protea cf. *welwitschii* Engl.	rare	dwarf shrub	geoxylic grassland (ferraliticsoils)	132480 (HBG)
Protea sp. 133045	rare	dwarf shrub	geoxylic grassland (sandy soils)	133045 (HBG)
Rhamnaceae				
Ziziphus mucronata Willd.	rare	shrub	woodland / forest	133093; 135285 (HBG)
Rubiaceae				
Ancylanthos rubiginosus Desf.	rare	dwarf shrub	geoxylic grassland (on sandy soils) & woodland ecotone	136003 (HBG)
Fadogia cf. *chrysantha* K.Schum.	very rare	shrub	woodland ecotone	134257 (HBG)
Fadogia cf. *triphylla* var. *triphylla* Baker	very rare	shrub	woodland / forest	132987 (HBG); 133081 (HBG)
Fadogia fuchsioides Welw. ex Oliv. (Figure 4c)	occasional	shrub	woodland / forest	132524 (HBG)
Fadogia cf. *homblei* De Wild.	rare	dwarf shrub / geoxyle	geoxylic grassland	140114 (LUBA)
Fadogia cf. *monticola* Robyns	rare	dwarf shrub / geoxyle	geoxylic grassland	140146 (LUBA)
Fadogia sp. 134097	occasional	shrub	geoxylic grassland (ferralitic soils), woodland ecotone	132453; 134097; 134167 (HBG)
Gardenia brachythamnus (K.Schum.) Launert	very rare	dwarf shrub	woodland ecotone	135338 (HBG)
Keetia cf. *gracilis* (Hiern) Bridson	very rare	shrub	woodland / forest	132442; 133148 (HBG)
Keetia venosa (Oliv.) Bridson	rare	shrub	woodland / forest	132534A (HBG)
Leptactina benguellensis (Welw. ex Benth. & Hook.f.) R.D.Good	rare	dwarf shrub	woodland / forest	135313; 135353; 133153 (HBG)
Leptactina prostrata K.Schum	very rare	dwarf shrub	geoxylic grassland (ferralitic soils)	134181 (HBG)
Pachystigma pygmaeum (Schltr.) Robyns	frequent	dwarf shrub / geoxyle	geoxylic grassland (sandy soils)	140138 (LUBA)
Pygmaeothamnus cf. *chamaedendrum* (Kuntze) Robyns	very rare	dwarf shrub	geoxylic grassland (sandy soils)	132723 (HBG)
Pygmaeothamnus sp. 132552	very rare	dwarf shrub	woodland / forest	132552 (HBG)
Pygmaeothamnus zeyheri (Sond.) Robyns	rare	dwarf shrub	geoxylic grassland (sandy soils)	132798; 133033; 134089 (HBG)
Rytigynia orbicularis (K.Schum.) Robyns	frequent	shrub	woodland / forest	132925; 134127 (HBG); 139056 (LUBA)
Tapiphyllum cf. *psammophilum* (S.Moore) Robyns	very rare	shrub	woodland / forest	134279 (HBG)
Tricalysia angolensis A.Rich. ex DC.	very rare	shrub	woodland / forest	132500; 133012 (HBG)
Tricalysia sp. 134221	rare	shrub	woodland / forest	134221 (HBG)
Tricalysia coriacea ssp. *nyassae* (Benth.) Hiern	occasional	shrub	woodland / forest	133008; 134095; 134170 (HBG)
Tricalysia sp. 135367	very rare	shrub	woodland / forest	135367 (HBG)
Santalaceae				
Thesium sp. 139228	rare	dwarf shrub	woodland / forest	139228 (LUBA)
Sapotaceae				
Chrysophyllum bangweolense R.E.Fr.	rare	tree	woodland / forest	135359 (HBG)
Englerophytum magalismontanum (Sond.) T.D.Penn.	common	shrub	woodland / forest	135320 (HBG); 133151 (HBG); 139109 (LUBA)
Smilacaceae				
Smilax anceps Willd.	rare	shrub	woodland / forest	135308A (HBG)
Strychnaceae				
Strychnos cocculoides Baker	frequent	shrub / tree	woodland / forest	139070 (LUBA)
Strychnos pungens Soler.	common	shrub / tree	woodland / forest	139254 (LUBA)
Strychnos spinosa Lam.	occasional	tree	woodland / forest	135301 (HBG)

field work for this study (Gonçalves et al. 2016). In the case of *Combretum schumannii* Engl. literature indicated that the range of the species might extend to Angola (Exell & Wild 1960). However, neither this taxon nor its synonyms were included in the Angolan checklist (Figueiredo & Smith 2008).

Most of the species occurred either in the geoxylic grasslands or in the woodlands and forests. However, many of the geoxylic suffrutices have closely related tree species growing nearby in the woodlands (Figures 4h and 4i). In Africa, the centre of diversity of geoxylic suffrutices is in the Zambezian phytoregion. In regions with similar environmental conditions, such as the Sudanian phytoregion, there is only a very limited number of geoxylic species (White 1976).

We found two types of geoxylic grasslands, each harbouring a very distinct species pool with only a small overlap. There is much debate on the environmental factors driving the emergence of this distinct life form (Davy 1922; White 1976; Maurin et al. 2014; Finckh et al. 2016). However, the different species composition of the two types of geoxylic grasslands found in Cusseque can be clearly attributed to the contrasting edaphic conditions. The two dominant species in the "geoxylic grasslands on ferralitic soils" *Cryptosepalum maraviense* (Figure 4g) and *C. exfoliatum* ssp. *suffruticans*

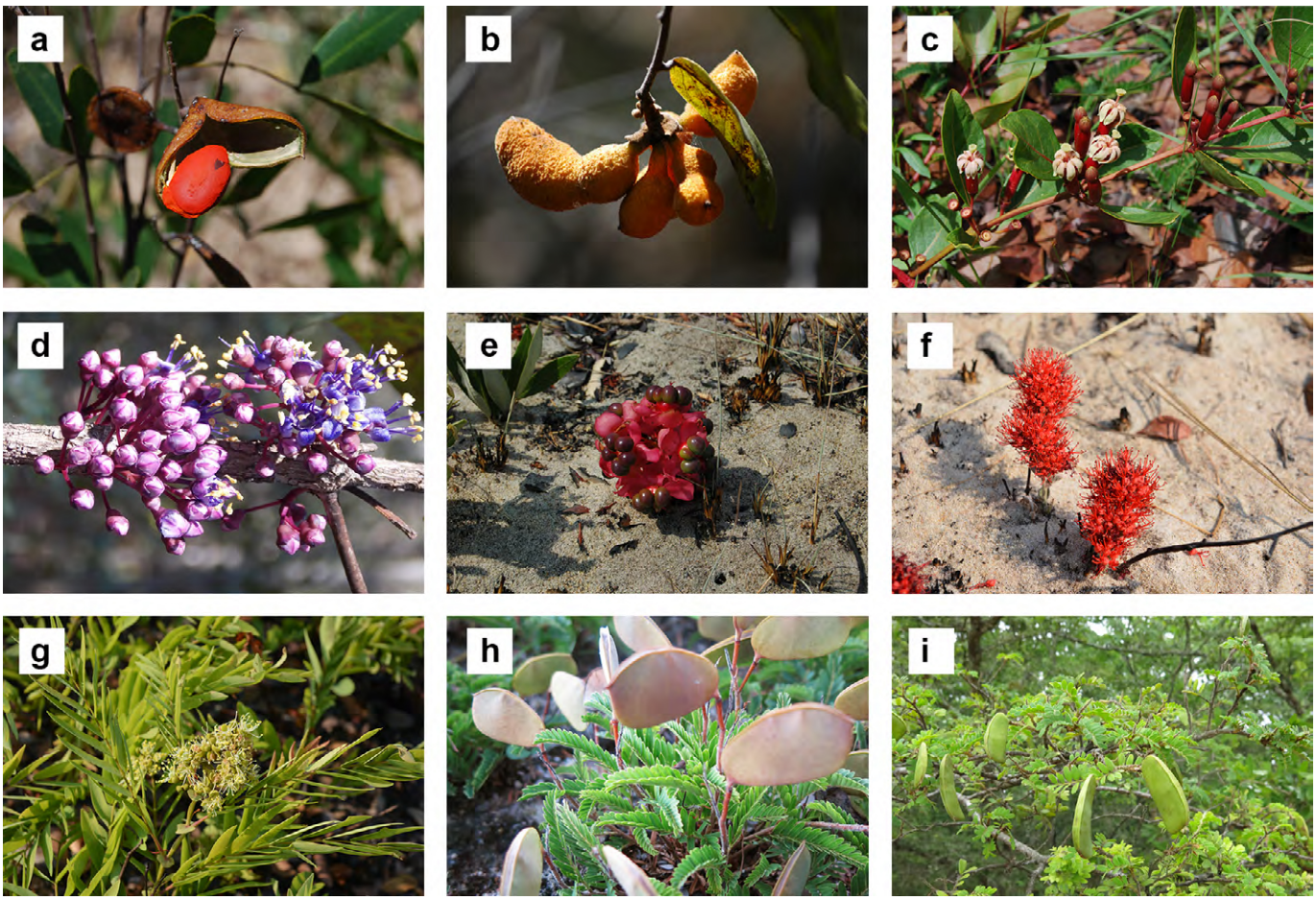

Figure 4 Typical plants of the Cusseque area: **a)** *Copaifera baumiana*, **b)** *Uvaria angolensis*, **c)** *Fadogia fuchsioides*, **d)** *Warneckea sapinii*, **e)** *Ochna arenaria*, **f)** *Combretum platypetalum* ssp. *platypetalum*, **g)** *Cryptosepalum maraviense*, **h)** *Cryptoseplaum exfoliatum* ssp. *suffruticans*, **i)** *Cryptosepalum exfoliatum* ssp. *pseudotaxus*.

(Figure 4i) belong to the Fabaceae. In contrast, the "geoxylic grasslands on sandy soils" were dominated by various species of the genus *Ochna* of the Ochnaceae and *Parinari capensis* of the Chrysobalanaceae. The "geoxylic grasslands on ferralitic soils" have their core distribution on the Angolan Central Plateau and make up 8.5% of the land surface within the Cubango Basin (Revermann et al. in revision). The "geoxylic grasslands on sandy soils" have a very limited distribution within the study site and cover 0.7% of the area of the Cubango Basin. However, they are more extensive further east in the Cuito River Basin and in eastern Moxico Province, where they occur on large sandy, alluvial plains of the Zambezi Graben, e.g., in Cameia National Park.

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