ERRATUM

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

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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.
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 m² 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 km². 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 Gosseweiler, 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, Gosseweiler produced the first phytogeographic map of Angola containing 19 principal vegetation types (Gosseweiler & Mendonça 1939). Based on this map and his own observations, Luis 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 km² (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 Plinthosols 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 suffrutes occur on two different soil types: on deep, leached sandy soils and on shallow, compact, ferrallitic soils. Accordingly, we will differentiate herein between “geoxylic grasslands on sandy soils” (Figure 2c) and “geoxylic grasslands on ferrallitic 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...
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...
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 geoxyl 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.

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 km² 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 km². 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 geoxyl 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 ctraegifolium (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 | geoxyle 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 | geoxyle grassland (ferralitic soils) | 140101 (LUBA) |
| Rhus exelliana Meikle | frequent | dwarf shrub | woodland / forest | 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 | geoxyle grassland (sandy soils) | 133044; 134116 (HBG); 140109 (LUBA) |
| **Annonaceae** | | | | |
| 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 Oliv. | frequent | shrub | woodland / forest | 133057A; 134263 (HBG) |
| Xylopia tomentosa Exell | common | shrub | woodland / forest | 135279; 132956; 132986; 139257; 132986 (HBG); 139177 (LUBA) |
| **Apocynaceae** | | | | |
| Chamaecitandra henriquesiana (Hallier f.) Pichon | common | dwarf shrub / geoxyle | geoxyle 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 | geoxyle 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) |
| **Crysantheaceae** | | | | |
| Parinari curatellifolia Harv. | frequent | dwarf shrub / geoxyle | geoxyle 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 eleanooides 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 / geoxyle | geoxyle grassland (sandy soils) | 132639; 134114; 140113 (HBG) |
| Combretum schumannii Engl. | rare | shrub | woodland / forest | 139048 (LUBA) |
| Pterolepis 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 | geoxyle grassland (sandy soils) | 140165 (LUBA) |
| **Dipterocarpaceae** | | | | |
| Monotes africanus A.DC. | common | tree | woodland / forest | 132917; 134160; 142228 (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 | shrub / geoxyle | geoxyle grassland (sandy soils) | 140179 (LUBA) |

Continued
### Table 1. Continued.

| Species name | Frequency | Life form | Habitat | Collection number(s) |
|--------------|-----------|-----------|---------|----------------------|
| **Ebenaceae, continued** | | | | |
| Diospyros pseudomespilus spp. brevicalyx Mildbr. | frequent | shrub | woodland / forest | 135379 (HBG) |
| Diospyros virgata (Gürke) Brenan | occasional | shrub | woodland / forest | 132941 (HBG) |
| Euclée crispa spp. crispa (Thunb.) Gürke | frequent | dwarf shrub | woodland / forest / geoxyle grassland | 135413 (HBG) |
| **Ericaceae** | | | | |
| Erica benguellensis (Welw. ex Engl.) E.G.H. Oliv. | very rare | shrub / tree | woodland / forest | 139235 (LUBA) |
| **Euphorbiaceae** | | | | |
| Bridelia sp. 130995 | occasional | shrub / tree | woodland / forest | 139095 (LUBA) |
| Hymenocardia acidica 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) |
| Sclerocoroton oblongifolius (Müll. Arg.) Kruijt & Roebers | frequent | dwarf shrub | woodland / forest | 132990; 134185 (HBG) |
| Uapaca sp. 134199 | common | dwarf shrub / geoxyle | geoxyle grassland (ferralitic soils) | 132490; 134199 (HBG) |
| Uapaca nitida var. nitida Müll. Arg. | common | tree | woodland / forest | - |
| Uapaca nitida | common | tree | woodland / forest | 132691; 132912; 132998 (HBG) |
| **Fabaceae** | | | | |
| Abrus melanoperus ssp. suffruticosus (Boutique) D.K.Harder | occasional | dwarf shrub / geoxyle | geoxyle 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 bequaerti De Wild. | frequent | shrub / tree | woodland / forest | 135360; 139242; 133018 (HBG) |
| Bauhinia petersoniana Bolle | common | shrub | woodland / forest | 135311 (HBG) |
| Babungnana 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 speciformis 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 florinda Welw. ex Baker | rare | dwarf shrub | woodland / forest | 139196 (LUBA) |
| Cryptosepalum exfoliatum ssp. pseudotoxus (Baker f.) P.A.Duvign. & Brenan | common | tree | woodland / forest | 135304 (HBG); 139023 (LUBA) |
| Cryptosepalum exfoliatum ssp. suffruticans (P.A.Duvign.) P.A.Duvign. & Bre (Figure 4f) | common | dwarf shrub | geoxyle grassland (ferralitic soils) | 132754; 132825 (HBG) |
| Cryptosepalum maraviesiens Oliv. (Figure 4g) | common | dwarf shrub | geoxyle grassland (ferralitic soils) | 135308B; 135620 (HBG) |
| Dolichos nitidulus 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 | geoxyle grassland (ferralitic soils) | 140088 (LUBA) |
| Entada arenaria Schinz | very rare | dwarf shrub | geoxyle grassland (sandy soils) | 134147 (HBG) |
| Erisesma sp. 133109 | rare | dwarf shrub | geoxyle grassland (ferralitic soils) | 133109 (HBG) |
| Erisesma sp. 132895 | rare | dwarf shrub | geoxyle 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) |
| Guiboura coleoperma (Benth.) J.Léonard | occasional | tree | woodland / forest | 139054 (LUBA) |
| Humulatera welwitschi (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) |
| Kotschy stroblantona (Welw. ex Baker) Dewit & P. A. Duvign. var. stroblantona | rare | dwarf shrub / geoxyle | geoxyle grassland (ferralitic soils) | 139141 (LUBA) |
| Mucuna sp. 140052 | frequent | dwarf shrub / geoxyle | geoxyle 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 lemoineanus* (De Wild. & T.Durand) T.Durand & H.Durand | common | shrub | woodland / forest | 132968; 133005; 133149 (HBG) |
| **Lamiaceae** |           |           |         |                      |
| *Alveia rosmarinifolia* Welw. | occasional | shrub | woodland / forest | 132509 (HBG); 139140 (LUBA) |
| *Alveia sp.* | occasional | shrub | woodland / forest | 132509 (HBG); 139140 (LUBA) |
| **Melastomataceae** |           |           |         |                      |
| *Mecoblogia praecox* (Welw.) E. Raynolds | frequent | dwarf shrub | geoxyle grassland (sandy soils) | 135381; 135796 (HBG) |
| *Mecoblogia perennis* Welw. | occasional | shrub | woodland / forest | 135309 (HBG); 139140 (LUBA) |
| **Melastomataceae** |           |           |         |                      |
| *Mecoblogia praecox* (Welw.) E. Raynolds | frequent | dwarf shrub | geoxyle grassland (sandy soils) | 135381; 135796 (HBG) |
| *Mecoblogia perennis* Welw. | occasional | shrub | woodland / forest | 135309 (HBG); 139140 (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 | geoxyle 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 | geoxyle grassland (sandy soils) | 132947; 133024 (HBG); 140154 (LUBA) |
| *Ochna manikensis* De Wild. | frequent | dwarf shrub | geoxyle grassland (sandy soils) | 132654; 132803 (HBG) |
| *Ochna pulchra* Hook. | common | shrub / geoxyle | woodland / forest | 135381; 139064 (LUBA); 139239; 140154 (LUBA) |
| **Oleaceae** |           |           |         |                      |
| *Jasminum pauciflorum* Bentham. | rare | liana / shrub | woodland / forest | 139238 (LUBA) |
| *Schebera trichocladia* Welw. | rare | shrub / tree | woodland / forest | 139189 (LUBA) |
| **Orobanchaceae** |           |           |         |                      |
| *Sapubia karaguensis* Oliv. | rare | dwarf shrub | woodland / forest | 139033 (LUBA) |
| **Passifloraceae** |           |           |         |                      |
| *Paropsia brazzaeana* Baill. | common | shrub | woodland / forest | 135299 (HBG); 139242 (LUBA) |
| **Picandraceae** |           |           |         |                      |
| *Oldfieldia dactylophylla* (Welw. ex Oliv.) J.Léonard | rare | shrub | woodland / forest | 139208 (LUBA) |
| **Polygalaceae** |           |           |         |                      |
| *Securidaca longepedunculata* Fresen | occasional | tree | woodland / forest | 133017 (HBG) |
| **Polygonaceae** |           |           |         |                      |
| *Oxygonum frutosum* Dammer ex Milne-Redh. | frequent | shrub | woodland / forest | 135322; 133032 (HBG); 139164 (LUBA) |
| **Proteaceae** |           |           |         |                      |
| *Faurea intermedii* Engl. & Gilg | occasional | shrub / tree | woodland / forest | 132720; 139072 (LUBA) |
| *Faurea rochetiensis* (A.Rich.) Chiov. ex Pic.Serm. | frequent | tree | woodland / forest / ecotone | 135307 (HBG) |
| *Faurea saligna* Harv. | occasional | tree | geoxyle grassland (ferralitic soils) | 132549; 132980; 134205 (HBG) |
| *Protea ballumi* Engl. & Gilg. | occasional | dwarf shrub | woodland / forest | 132501; 133019; 134225 (HBG) |
| *Protea gageoidi* J.F.Gmel. | frequent | tree | woodland / forest | 132918 (LUBA) |
| *Protea angolensis* var. *divaricarta* (Engl. & Gilg.) Beard | rare | dwarf shrub | geoxyle grassland (ferralitic soils) | 134200 (HBG) |
| *Protea micans* ssp. *trichophylla* Welw. | occasional | dwarf shrub | geoxyle grassland (sandy soils) | 132607 (HBG); 140096 (LUBA) |
| **Proteaceae, continued** |           |           |         |                      |
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 geoxyc grasslands or in the woodlands and forests. However, many of the geoxyc suffrutes have closely related tree species growing nearby in the woodlands (Figures 4b and 4l). In Africa, the centre of diversity of geoxyc suffrutes is in the Zambezian phytoregion. In regions with similar environmental conditions, such as the Sudanian phytoregion, there is only a very limited number of geoxyc species (WHITE 1976).

We found two types of geoxyc 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 geoxyc 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

### 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 | geoxyc grassland | 132480 (HBG) |
| Protea sp. 133045 | rare | dwarf shrub | geoxyc grassland (sandy soils) | 133045 (HBG) |
| Rhamnaceae | | | | |
| Zuphis mucronata Wild. | rare | shrub | woodland / forest | 133093; 135285 (HBG) |
| Rubiaceae | | | | |
| Acanthos subetinoginosus Desf. | rare | dwarf shrub | geoxyc grassland (on sandy soils) & woodland ecotone | 136003 (HBG) |
| Fadogia cf. chrysanthia 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 fuscifoliosa Welw. ex Oliv. (Figure 4c) | occasional | shrub | woodland / forest | 132524 (HBG) |
| Fadogia cf. homblei De Wild. | rare | dwarf shrub / geoxyle | geoxyc grassland | 140114 (LUBA) |
| Fadogia cf. monticola Robyns | rare | dwarf shrub / geoxyle | geoxyc grassland | 140146 (LUBA) |
| Fadogia sp. 134097 | occasional | shrub | geoxyc 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 | 122534A (HBG) |
| Leptactina benguellensis (Welw. ex Benth. & Hook.f.) R.D.Good | frequent | dwarf shrub | woodland / forest | 135313; 135353; 133153 (HBG) |
| Leptactina prostrata K.Schum. | very rare | dwarf shrub | geoxyc grassland (ferralitic soils) | 134181 (HBG) |
| Pachystigma pygmaea (Schltr.) Robyns | frequent | dwarf shrub / geoxyle | geoxyc grassland (sandy soils) | 140138 (LUBA) |
| Pygmaeothamnus cf. chamaedendrum (Kuntze) Robyns | very rare | dwarf shrub | geoxyc grassland (sandy soils) | 132723 (HBG) |
| Pygmaeothamnus sp. 132552 | very rare | dwarf shrub | geoxyc grassland (sandy soils) | 132552 (HBG) |
| Pygmaeothamnus zeyheri (Sond.) Robyns | rare | dwarf shrub | geoxyc 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 cornacea 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) |
| Englerophyta magalismontana (Sond.) T.D.Penn. | common | shrub | woodland / forest | 133520 (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) |
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) Cryptosepalum exfoliatum ssp. suffruticos, i) Cryptosepalum exfoliatum ssp. pseudotaxus.

(Figure 4i) belong to the Fabaceae. In contrast, the “geoxyllic grasslands on sandy soils” were dominated by various species of the genus Ochna of the Ochnaceae and Parinari capensis of the Chrysobalanaceae. The “geoxyllic grasslands on ferrallitic 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 “geoxyllic 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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Woody species of the Miombo woodlands and geoxyllic 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 geoxyllic 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 m² 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 km². The study represents the first comprehensive account of the woody vegetation of the area including all habitats and growth forms.

Key words: Angola; Bié; geoxyllic 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, Luis 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 km² (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 Gleyisols 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.)
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 Figüeiredo & 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 Zambeziana* (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 Huila (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 geoxylia 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.

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 km² 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 km². 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 geoxylia 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 (HUNTELY & 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 | geoxyle 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 | geoxyle grassland (ferralitic soils) | 140101 (LUBA) |
| Rhus exelliana Meikle | frequent | dwarf shrub | woodland / forest | 135250; 134275 (HBG) |
| Rhus gracilipes Exell | frequent | dwarf shrub | woodland / forest | 139227; 132483 (HBG) |
| Rhus kirkii Oliv. | frequent | dwarf shrub | woodland / forest | 139253 (LUBA) |
| **Anisophyllaceae** | | | | |
| Anisophyllea boehmii Engl. | frequent | tree | woodland / forest | 134316; 139018; 135297 (HBG) |
| Anisophyllea quangensis Engl. ex Henriq. | rare | dwarf shrub | geoxyle grassland (sandy soils) | 133044; 134116 (HBG); 140109 (LUBA) |
| **Annonaceae** | | | | |
| 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 Oliv. | 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 | geoxyle 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 | geoxyle 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 | geoxyle 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 lasianthus 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 | geoxyle 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. | frequent | tree | woodland / forest / grassland (sandy and ferralitic soils) | 132997; 134088; 134131 (HBG) |
| **Dichapetalaceae** | | | | |
| Dichapetalum cymosum (Hook.) Engl. | frequent | dwarf shrub / geoxyle | geoxyle 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 dosyanthus 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 | geoxyle 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 / geoxyle 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) |
| Hymenocarpus acidu 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) |
| Pseudalocynostylis maprouneifolia Pax | occasional | tree | woodland / forest | 132555; 134232 (HBG); 139038 (LUBA) |
| Scleroaiton oblongifolius (Müll. Arg.) Kruj & Roebers | frequent | dwarf shrub | woodland / forest | 132990; 134185 (HBG) |
| Uapaca sp. 134199 | common | dwarf shrub / geoxyle | geoxyle grassland (ferralitic soils) | 132490; 134199 (HBG) |
| Uapaca nitida var. nitida Müll. Arg. | common | tree | woodland / forest | - |
| **Fabaceae** | | | | |
| Abrus melanospermus ssp. suffruticosus (Boutique) | occasional | dwarf shrub / geoxyle | geoxyle grassland (sandy soils) | 140167 (LUBA) |
| D.K.Harder | | | | |
| Albizia antunesiana Harms | frequent | tree | woodland / forest | 134156; 135318 (HBG); 139223 (LUBA) |
| Albizia gummarifera (J.F.Gmel.) C.A.Sm. | occasional | shrub / tree | woodland / forest | 139065; 135342; 132967 (HBG) |
| Baphia bequaerti De Wild. | frequent | shrub / tree | woodland / forest | 135360; 139242; 133018 (HBG) |
| Bauhinia petersoniana Bolle | common | shrub | woodland / forest | 135311 (HBG) |
| Babylonia madagascariensis (Desv.) J.H.Kirkbr. & Wiersema | frequent | shrub / tree | woodland / forest | 132963; 139128 (LUBA) |
| Brachystegia bakieriana 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 | - |
| Copalifera 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 flava 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 | geoxyle grassland (ferralitic soils) | 132754; 132825 (HBG) |
| Cryptosepalum maravisiense Oliv. (Figure 4g) | common | dwarf shrub | geoxyle grassland (ferralitic soils) | 135308B; 135620 (HBG) |
| Dalbergia nitida Welw. ex Baker | rare | shrub / tree | woodland / forest | 139236 (LUBA) |
| Dialium englerianum Henrici. | frequent | shrub / tree | woodland / forest | 133147; 139034 (LUBA) |
| Dolichos sp. 140088 | frequent | dwarf shrub / geoxyle | geoxyle grassland (ferralitic soils) | 140088 (LUBA) |
| Entada arenaria Schinz | very rare | dwarf shrub | geoxyle grassland (sandy soils) | 134147 (HBG) |
| Eriosema sp. 133109 | rare | dwarf shrub | geoxyle grassland (ferralitic soils) | 133109 (HBG) |
| Eriosema sp. 132895 | rare | dwarf shrub | geoxyle 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) |
| Guiboutia coleosperma (Benth.) J.Leonard | occasional | tree | woodland / forest | 139054 (LUBA) |
| Humuliera 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) |
| Kotschy streblonotha (Welw. ex Baker) Dewit & P.A. Duvign. var. streblonatha | rare | dwarf shrub / geoxyle | geoxyle grassland (ferralitic soils) | 139141 (LUBA) |
| Mucuna sp. 140052 | frequent | dwarf shrub / geoxyle | geoxyle grassland (sandy soils) | 140052 (LUBA) |
| Periposis angolensis (Baker) Meeuwen | frequent | shrub / tree | woodland / forest | 139181 (LUBA) |
| Pterocarpus angolensis DC | occasional | tree | woodland / forest | - |
| 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) |
| Ionanthaceae |           |           |         |                      |
| Phyllicosmus lemoineanus (De Wild. & T.Durand) T.Durand & H.Durand | common | shrub | woodland / forest | 132968; 133005; 133149 (HBG) |
| Lamiaceae |           |           |         |                      |
| Alvesia rosmarinifolia Welw. | occasional | shrub | woodland / forest | 134776; 132533 (HBG) |
| Tinnea sp. 133121 | frequent | dwarf shrub | geosync 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 | shrub | woodland / forest | 133039 (HBG); 139140 (LUBA) |
| Meliaceae |           |           |         |                      |
| Ekebergia benguelensis | rare | dwarf shrub | wetland margin | 141510 (HBG) |
| Moraceae |           |           |         |                      |
| Ficus pygmaea Welw. ex Hiern | rare | dwarf shrub | wetland margin | 141539 (HBG) |
| Myricaceae |           |           |         |                      |
| Morella cf. serrata (Lam.) Killick | rare | dwarf shrub / geoxyle | geosync 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 | geosync 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, geosync grassland (sandy and ferralitic soils) | 132947; 133024 (HBG); 140016 (LUBA) |
| 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 trichocladia Welw. | rare | shrub / tree | woodland / forest | 139189 (LUBA) |
| Orobanchaceae |           |           |         |                      |
| Sopubia karaguensis Oliv. | rare | dwarf shrub | woodland / forest | 139033 (LUBA) |
| Passifloraceae |           |           |         |                      |
| Paropsis brazzaeana Baill. | common | shrub | woodland / forest | 135299 (HBG); 139242 (LUBA) |
| Picondendraceae |           |           |         |                      |
| Oldfiedia dactylophylla (Welw. ex Oliv.) J.Léonard | rare | shrub | 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 | 133522; 133032 (HBG); 139164 (LUBA) |
| Proteaceae |           |           |         |                      |
| Faurea intermedia Engl. & Gilg | occasional | shrub / tree | woodland / forest | 133720; 139072 (LUBA) |
| Faurea rochetiana (A.Rich.) Chiov. ex Pic.Serm. | frequent | tree | woodland / forest / ecotone | 133507 (HBG) |
| Faurea saligna Harv. | occasional | tree | geosync grassland (ferralitic soils) | 132549; 132980; 134205 (HBG) |
| Protea baumii Engl. & Gilg. | occasional | dwarf shrub | woodland / forest | 132501; 133019; 134225 (HBG) |
| Protea gagnepu J.F.Gmel. | frequent | tree | woodland / forest | 132918 (LUBA) |
| Protea angolensis var. divaricarta (Engl. & Gilg.) Beard | rare | dwarf shrub | geosync grassland (ferralitic soils) | 134200 (HBG) |
| Protea micans ssp. trichophylophilus Welw. | occasional | dwarf shrub | geosync grassland (sandy soils) | 132607 (HBG); 140096 (LUBA) |

**Table 1. Continued.**

Continued
Most of the species occurred either in the geoxylic grasslands or in the woodlands and forests. However, many of the geoxylic suffrutescences have closely related tree species growing nearby in the woodlands (Figures 4h and 4i). In Africa, the centre of diversity of geoxylic suffrutescences 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 ferrallitic soils” Cryptosepalum maraviense (Figure 4g) and C. exfoliatum ssp. suffrutescens.
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) *Cryptosepalum exfoliatum* ssp. *suffruticans*, i) *Cryptosepalum exfoliatum* ssp. *pseudotaxus.*

(Figure 4i) belong to the Fabaceae. In contrast, the “geoxyllic grasslands on sandy soils” were dominated by various species of the genus *Ochna* of the Ochnaceae and *Parinari capensis* of the Chrysobalanaceae. The “geoxyllic grasslands on ferralic 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 “geoxyllic 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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