Research Article

Suffrutex grasslands in south-central Angola: belowground biomass, root structure, soil characteristics and vegetation dynamics of the 'underground forests of Africa'

Amândio L. Gomes[1,2,*], Rasmus Revermann[2,3], Francisco M. P. Gonçalves[2,4], Fernanda Lages[4], Marcos P. M. Aidar[5], Graciela A. Sanguino Mostajo[2] and Manfred Finckh[2]

[1]Faculty of Sciences, Agostinho Neto University, Av. 4 de Fevereiro 71 C.P. 815 Luanda, Angola; [2]Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology, University of Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany; [3]Faculty of Natural Resources and Spatial Sciences, Namibia University of Science and Technology, Windhoek, Namibia; [4]Herbarium of Lubango, ISCED Huíla, Department of Natural Sciences, Sarmento Rodrigues str., C.P. 230 Lubango, Angola and [5]Plant Physiology and Biochemistry, Institute of Botany, CP 3005 CEP 01061-970, São Paulo, Brazil

Abstract

Despite its importance for carbon stocks accounting, belowground biomass (BGB) has seldom been measured due to the methodological complexity involved. In this study, we assess woody BGB and related carbon stocks, soil properties and human impact on two common suffrutex grasslands (*Brachystegia-* and *Parinari* grasslands) on the Angolan Central Plateau. Data on BGB was measured by direct destructive sampling. Soil samples were analysed for select key parameters. To investigate vegetation dynamics and human impact, we used Moderate Resolution Imaging Spectroradiometer (MODIS) Enhanced Vegetation Index (EVI) and fire data retrieved via Google Earth Engine. Mean belowground woody biomass of sandy *Parinari* grasslands was 17 t/ha and 44 t/ha in ferralitic *Brachystegia* grasslands of which 50% correspond to carbon stocks. As such, the BGB of *Brachystegia* grasslands almost equals the amount of aboveground biomass (AGB) of neighbouring miombo woodlands. Almost the entire woody BGB is located in the top 30 cm of the soil. Soils were extremely acid, showing a low nutrient availability. Both grassland types differed strongly in EVI and fire seasonality. The *Parinari* grasslands burnt almost twice as frequent as *Brachystegia* grasslands in a 10-year period. Our study emphasizes the high relevance of BGB in suffrutex grasslands for carbon stock accounting.

Introduction

Patterns of aboveground biomass (AGB) distribution in terrestrial ecosystems are reasonably well understood, whereas interest in belowground biomass (BGB) and its distribution has risen only in recent years (IPCC 2006, Ravindranath and Ostwald 2008, Rosillo-Calle *et al.* 2007). However, BGB contributes strongly to the total plant biomass for many plant communities (Cairns *et al.* 1997, Chidumayo 2013, de Castro and Kauffman 1998, Grace *et al.* 2006, IPCC 2006, Ryan *et al.* 2010). Probably due to the difficulties in harvesting and measuring belowground organs, less attention has been given to BGB and methods of analysis have not been standardized (IPCC 2006, Lichacz *et al.* 2009, Sanford and Cuevas 1996, Wetzel and Howe 1999).

Yet, AGB and BGB both are important components of terrestrial ecosystem carbon stocks (Mokany *et al.* 2006). AGB, the most visible of all carbon pools, includes all biomass in living vegetation, both woody and herbaceous, above the soil including stems, stumps, branches, bark, seeds and foliage, whereas BGB is the entire biomass of all living roots, tubers, bulbs and rhizomes, excluding fine roots less than 2 mm in diameter because empirically, these cannot be easily distinguished from other components (Ravindranath and Ostwald 2008).

BGB is an important carbon pool for many vegetation types, ecosystems and land-use systems. Globally, BGB has a high share of total biomass in most grassland ecosystems (Coupland 1992). In addition, many tropical grasslands are co-dominated by geoxylic suffrutices (du Rietz 1931; White 1976) or geoxyles (Lindman 1914; Simon *et al.* 2009), e.g. in the Brazilian cerrado or in the miombo woodland landscapes of south-central Africa. Geoxyles are small woody plants with annual or short-lived woody shoots sprouting from massive or extensive perennial woody underground axes (White 1976), comprising xylopodia (Simon *et al.* 2009), lignotubers (Kolbek and Alves 2008) or woody rhizomes (Pausas *et al.* 2018). Most geoxylic biomass is located below

ground (Robertson, 2005) in a complex network of rhizomes, roots, or tubers, and thus was referred to as 'underground forests' by White (1976) in his pioneering paper on geoxylic suffrutices.

The Zambezian centre of endemism is a hotspot of geoxyle diversity (White 1976), but the reasons for this surprising diversity are still not well understood (Zigelski et al. 2019). On the Angolan Central Plateau, suffrutex grasslands cover a substantial part of the land surface (Stellmes et al. 2013a). While miombo woodlands grow on the hills and upper slopes, the lower slopes of most valleys are covered by open vegetation types dominated by grasses and geoxyles. Thus, to correctly quantify carbon allocation and storage of these particular ecosystems, BGB has to be taken into account.

Obtaining accurate estimates of BGB is recognized as essential for determining its contribution to carbon storage (Chamberlain et al. 2013), and thus required for reporting to the United Nations Framework Convention on Climate Change and REDD+. So far, most inventories have used an average root-to-shoot ratio and allometric equations to estimate BGB for several purposes such as carbon accounting (Chidumayo 2013, Nieto-Quintano et al. 2018, Ryan et al. 2010). However, none of these methods can be applied to suffrutex grasslands due to the great difference between above and belowground organs (Robertson 2005). Thus, direct, destructive sampling is the only method to obtain accurate estimates of BGB of suffrutex grasslands. To our knowledge, BGB of suffrutex grasslands has so far not being quantified by direct sampling in the African tropics. Therefore, in this paper, we aim (1) to shortly describe and compare the ecology, structure and phenology of the two main types of suffrutex grasslands in central Angola; (2) to describe habitat preferences and morphology of the dominant geoxyle species of these two habitat types; (3) to assess BGB and carbon stocks of the suffrutex grasslands; (4) to discuss the relationship between BGB, soil properties and geoxyle morphology; and (5) to briefly assess current human impacts on suffrutex grasslands. The results will allow us to better understand the ecological importance of suffrutex grasslands and their role in the functioning of African savannas, which are still strongly data deficient (Ryan et al. 2010).

Study site

The study was conducted in the Cusseque area of the Chitembo Municipality in Bié Province, Angola (Figure 1a–d). The elevation of the study area varies between 1397 m and 1562 m. The landscape is dominated by miombo woodlands (main tree species belong to the Fabaceae genera *Brachystegia*, *Cryptosepalum*, *Julbernardia* and *Isoberlinia*). The vegetation distribution follows the topography of the landscape. While the hill tracts are dominated by closed-canopy woodlands, the valleys are dominated by geoxylic grasslands. In this area, two types of geoxylic grassland can be distinguished: *Brachystegia russelliae*-dominated 'Anharas de Ongote', hereafter called *Brachystegia* grasslands on ferralitic soils of the east–west running tributary rivers and *Parinari capensis*-dominated 'Chanas de borracha', hereafter called *Parinari* grasslands on sandy deposits of the main north–south stretching Cusseque valley (Revermann et al. 2013, 2017, 2018). *Brachystegia* grasslands cover 23.3% of the study site and *Parinari* grasslands 8.5% (Schneibel et al. 2013). The diversity of geoxyles in both grassland types is high. Zigelski et al. (2019) report more than 121 species of geoxyles for Angola of which more than 70 species occur in the study area (Revermann et al. 2017; own unpublished data).

The study area has a subhumid summer rainfall climate with a pronounced wet season lasting from October to April with a mean annual precipitation of 987 mm. Mean annual temperature is 20.4° C (Weber 2013). Night frosts occur frequently during the winter (June and July) especially in the valleys (Revermann & Finckh 2013, Finckh et al. 2016).

Material and Methods

Seasonal vegetation dynamics of suffrutex grasslands in central Angola

We used data from the Moderate Resolution Imaging Spectroradiometer (MODIS) to compare the seasonal land cover dynamics of *Brachystegia*- and *Parinari* grasslands. For 20 sites systematically distributed over the suffrutex grasslands of the study area (10 in each vegetation unit), we used the Google Earth Engine to retrieve the Enhanced Vegetation Index (EVI) based on the combined MYD13Q1 and MOD13Q1 data products covering the observation period 2010–2019. The systematic sampling design was chosen to cover all main grassland tracts separated by fire breaks (forests, wetlands, roads) and to minimize the probability that several sampling points were affected by single fire events. To analyse the phenological development and to obtain a proxy for the (AGB) throughout the season, we calculated the mean annual course of the EVI for both vegetation types over the 10-year period.

Structure and morphology of woody belowground plant organs

The area covered by suffrutex grasslands exhibited two characteristic soil types, ferralitic and sandy soils. For each of the two present soil types, we chose the three most dominant geoxyle species for structural and morphological analyses. In ferralitic soils, these were *Brachystegia russelliae* I. M. Johnston, *Cryptosepalum exfoliatum* subsp. *suffruticans* (P. A. Duvign.) P. A. Duvign. and Brenan and *Syzygium guineense* subsp. *huillensis* (Hiern.) F. White; in the sandy soil, we chose *Parinari capensis* Harv., *Pygmaeothamnus zeyheri* (Sond.) Robyns and *Ochna arenaria* De Wild. and T. Durand. We excavated five individuals of each species. During excavation, we carefully removed the soil around the individuals with a shovel, knife and by hand, striving for the extraction of intact belowground organs (roots, shoots, tubers and buds). We observed and described in detail their complex woody belowground structures and morphology. For classification of the belowground bud bank (BBB) type, we followed Pausas et al. (2018). The taxon which we call in this paper *Cryptosepalum exfoliatum* subsp. *suffruticans* (P. A. Duvign.) P. A. Duvign. and Brenan does not fully match the description in Flora Zambesiaca. Specimens have been deposited at the herbaria LUBA and HBG under the collection numbers 132481, 132685, 132754, 132825, 133059, 134697 and 143366. D. Goyder and R. Polhill (both at Royal Botanic Gardens, Kew) consider it as a putative new *Cryptosepalum* species (pers. comm.). However, in order to maintain consistency with previous publications (e.g. Gomes et al. 2019, Revermann et al. 2013, 2017, 2018, Zigelski et al. 2019), for the time being we continue to use the name.

Belowground biomass and carbon stocks

BGB per unit area was assessed based on field measurements of samples collected in 138 square pits dug within the study area (99 in *Brachystegia* grasslands and 39 in *Parinari* grasslands), harvesting all woody biomass. Pits were distributed in the following order: 60 pits (all in *Brachystegia* grasslands) were located in 2 1,000 m² (20 m × 50 m) plots divided into 10 subplots of
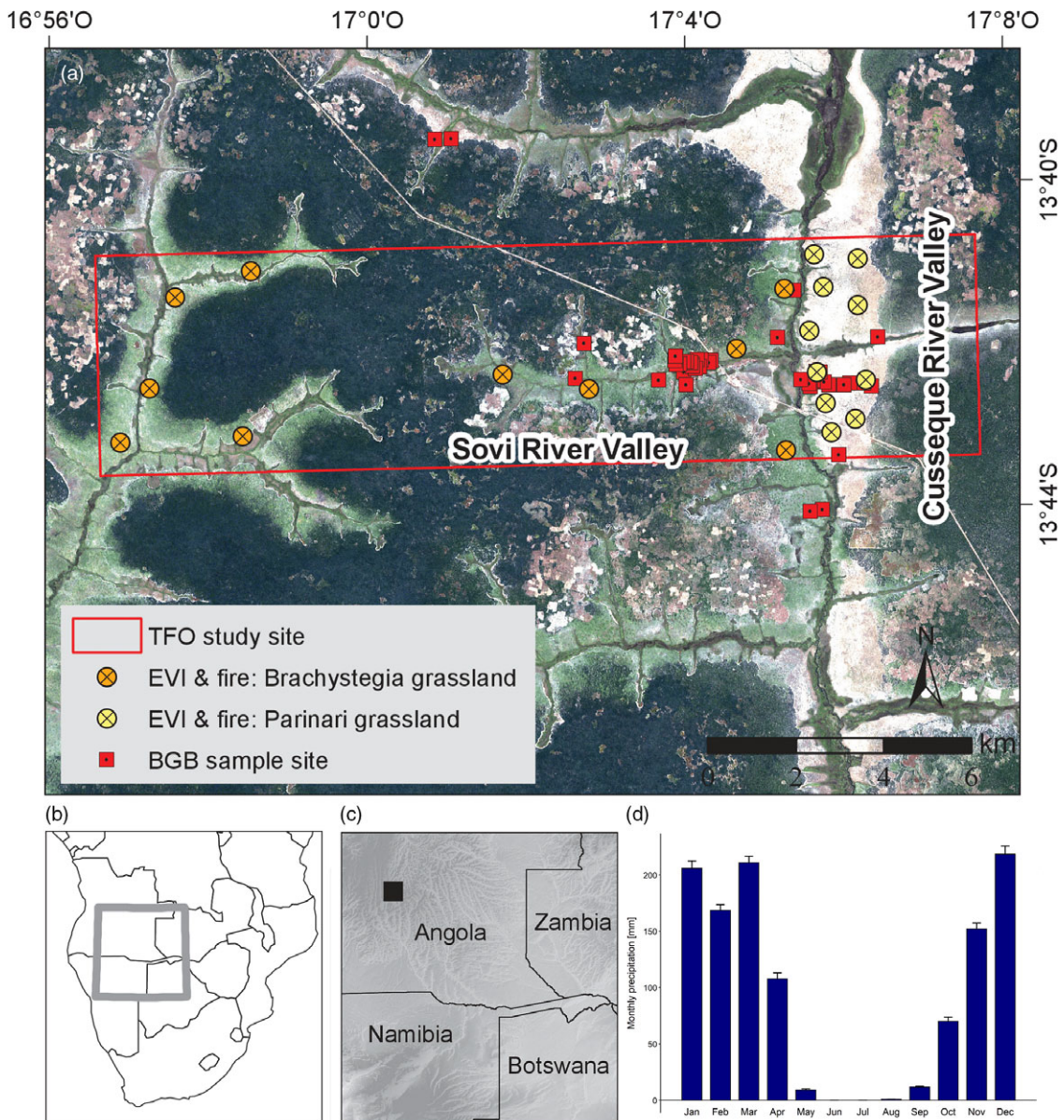
Figure 1. (a) The research site Cusseque of The Future Okavango (TFO) project (www.future-okavango.org) in the upper Cubango basin (red rectangle, 100 km²). The occurrence of open suffrutex grasslands on ferralitic soils (light green colour, e.g. in the Sovi River valley) and sandy deposits (white, eastern bank of the Cusseque River) is a characteristic feature in the valleys, contrasting with the miombo woodlands on the hills (dark green); (b) location in south-central Africa (the Okavango Basin marked with grey square); (c) the Cubango/Okavango Basin in the three countries Angola, Namibia and Botswana, black square indicates the research site Cusseque; (d) mean monthly rainfall in the study area (Fick and Hijmans 2017).

10 m × 10 m each; for each subplot, we dug 3 pits of 0.5 m × 0.5 m × 0.5 m (length, width and depth) diagonally, with 2 pits in the opposite corners and 1 in the centre (Dengler 2009) as shown in Figure S1. Furthermore, 48 pits (36 in *Brachystegia* grasslands and 12 in *Parinari* grasslands) of the same size were located in 16 plots of 10 m × 10 m spread in the geoxylic grasslands (12 in *Brachystegia* grasslands and 4 in *Parinari* grasslands); 20 pits (3 in *Brachystegia* grasslands and 17 in *Parinari* grasslands) were dug randomly in surrounding grasslands. Despite the highest woody biomass concentration being in many vegetation types in a depth of 0.3 m (de Castro and Kauffman 1998, Jackson *et al.* 1996, Ravindranath and Ostwald 2008), we harvested down to 0.5 m to include almost all BGB. Before digging, each pit was cleared of all AGB with pruning shears. During excavation, all woody roots and/or branches > 2 mm in diameter were carefully

separated from the soil material. All harvested biomass was dried to constant weight. Dry mass was obtained using a digital scale, after eliminating the last remnants of soil material. For sake of comparability with data from the literature, all weights are given as t/ha.

Carbon stocks were estimated assuming that 50% of the biomass corresponds to carbon (Ciais *et al.* 2011, IPCC 2006, Nabuurs *et al.* 2003, Schlesinger 1997). We used the measured dry mass to calculate the corresponding carbon stock in suffrutex grasslands.

Soil characteristics

Soil samples were taken in the centre of 46 plots (18 in ferralitic soils and 28 in sandy soils). Soil samples were taken at three depths: (1) 0 cm–10 cm; (2) 10 cm–30 cm; (3) 30 cm–50 cm. Soil analyses

were made in the soil laboratory of the Instituto de Investigação Agronómica da Chianga, in Huambo, Angola. For each layer, we analysed texture (particle size class distribution by sedimentation test), pH (by potentiometer in water, KCl and $CaCl_2$), exchangeable bases (EB) (by ammonium acetate method), exchangeable acidity (Al+H) (by KCl extraction), cation exchange capacity (CEC) by calculation (CEC=K+Ca+Mg+(H+Al)), extractable phosphorous (by Truog method), aluminium saturation (m) by calculation (m=100*Al^{3+}/CEC), total exchangeable bases (TEB) by calculation (TEB=K^++Ca^{2+}+Mg^{2+}+Na^+) and base saturation (V) by calculation (V=100*TEB/CEC). Subsequently, we calculated the average of each parameter per plot and finally, the mean for the study area was calculated.

Human impact

Since 2011, we conducted field research on the southern slopes of the Bié Plateau, visiting the wider study area at least twice a year. Since then, we continuously surveyed the study area for human activities affecting the woodlands (including suffrutex grasslands) and observed changes in land-use practices. Of particular importance are human-made fires, which are often used in the study area during the dry season to facilitate hunting of small game. To quantify the fire frequency in the suffrutex grasslands and to compare fire dynamics between the vegetation units, we again used data from the MODIS. For the same 20 sites as used for the EVI, we retrieved the MCD64A1 Version 6 Burned Area data product to assess the seasonal fire of *Brachystegia*- and *Parinari* grasslands. Based on the 10-year period from 2010 to 2019, we calculated for both vegetation types the seasonal mean monthly fire incidence per plot.

Data analyses

One-way ANOVA was used to test for significant differences in mean values of BGB and soil properties between the two different grassland types. All statistical analyses were carried out using BioEstat (Version 2.0) and PAST (Version 2.16).

Results

Ecology, structure and seasonal vegetation dynamics of the two main types of suffrutex grasslands in central Angola

The suffrutex grasslands of the study area are subject to strong seasonal changes. Field observations indicate that geoxyles dominate from mid-August to December while grasses shape the appearance from January to June. Senescence of the leaves of geoxyles and grasses occurs in the cold dry season from mid-May to mid-August. The EVI curves of both vegetation types clearly depict this general seasonal pattern with the lowest values observed in July, corresponding to the peak of the dry season, a marked increase in September already prior to the onset of the rainy season, and the peak in December and January (Figure 2a and b).

However, throughout the year, the EVI of *Brachystegia* grasslands is considerably higher than the EVI of *Parinari* grasslands. This higher EVI reflects the dense (micro-) canopy cover and high leaf biomass of the dominant *Brachystegia russelliae*, which has no equivalent in the *Parinari* grasslands (Figure 2).

Structure and morphology of complex belowground organs

The six geoxyle species displayed a wide spectrum of belowground organs in terms of their morphology, spatial distribution and area occupied, despite being encountered under similar environmental conditions (Table 1). However, all species showed BBB (Pausas *et al.* 2018) in the thickened underground woody organs from which new aerial shoots regenerate after die-off of aboveground shoots through local disturbance such as fire, frost or herbivory.

Table 1 describes the habitat preferences and the morphology of the dominant geoxyle species based on in situ measurements. The first three species dominate the ferralitic *Brachystegia* grasslands in the east–west stretching tributary valleys, the following three are characteristic of the *Parinari* grasslands in the north–south stretching main valley of the study area (Figure 1). Examples of the underground organs of the studied species are shown in Figure 3a–f.

Belowground biomass and carbon stocks

BGB varied considerably within and between the two types of geoxylic grassland. In *Parinari* grasslands, BGB varied from 0.56 to 45.60 t/ha with an average and standard error of 16.61±3.05 t/ha, while in *Brachystegia* grasslands on ferralitic soil, BGB varied from 4.56 to 95.20 t/ha with an average and standard error of 44.25±3.99 t/ha (Table S1 and Figure 4). One-way ANOVA showed that BGB in *Brachystegia* grasslands was significantly higher than in *Parinari* grasslands (F=25; p<0.001). Assuming that 50% of the biomass is carbon (Ciais *et al.* 2011, Nabuurs *et al.* 2003, Schlesinger, 1997), we can estimate that BGB-associated carbon stocks in *Parinari*- and *Brachystegia* grasslands are equivalent to 8.30 t/ha and 22.12 t/ha, respectively.

Soil properties

Our analyses revealed that the soils in the study sites are extremely acidic, with low clay and high sand content, low contents of the main EB (K, Mg and Ca) and base saturation (V), very low CEC, very low exchangeable phosphorus and consequently very low soil fertility. Aluminium was the cation dominating CEC and sodium was completely absent in all soil samples from suffrutex grasslands (Table S2).

Comparing the two grassland types (Table 2), one-way ANOVA revealed significant differences in soil properties: Sand content and pH_{KCl} were higher in *Parinari*- than in *Brachystegia* grasslands, while pH_{CaCl2}, K, Ca, P, Al+H, CEC and EB were higher in *Brachystegia*- than in *Parinari* grassland soils. In general, sand content in *Parinari* grassland soils (92.3%) was higher than in *Brachystegia* grassland soils (84.6%). Clay content was very low (2.9%) in *Parinari* grassland soils and but slightly higher in *Brachystegia* grassland soils (5.6%). However, clay content did not show a constant vertical distribution pattern in the soil profiles (Tables S1 and S2).

Human impact on geoxylic grassland

To date, the main human impacts in both types of suffrutex grasslands are anthropogenic dry season fires. The analysis of fire frequency based on MODIS time series data showed that over a 10-year period, *Parinari* grassland sites experienced a much higher mean annual fire incidence (0.70±0.058 fires per year) than *Brachystegia* grassland sites (0.37±0.086 fires per year), meaning that *Parinari* grasslands burn in 2 out of 3 years while *Brachystegia* grasslands burn only (a bit more than) once in 3 years. These data for fire incidence are minimum values as small patchy fires might go undetected in the MODIS Burned Area data product with a resolution of 500 m. Besides that, the fire season in *Parinari*

Table 1. Habitat preferences and morphological description of selected geoxyle species

	Brachystegia russelliae	*Cryptosepalum exfoliatum* subsp. *suffruticans*	*Syzygium guineense* subsp. *huillense*	*Parinari capensis*	*Pygmaeothamnus zeyheri*	*Ochna arenaria*
Soil type	Ferralitic	Ferralitic	Ferralitic and sandy	Sandy	Sandy	Sandy
BBB type*	Woody rhizome	Woody rhizome	Lignotuber	Woody rhizome	Woody rhizome	Woody rhizome
Growth direction	Horizontal, interwoven, two layers	Horizontal, interwoven, up to four layers	Lignified tubers, few thickened ramifications	Horizontal, wide stretching	Horizontal, wide stretching	Horizontal
N	29	29	12	14	19	17
Mean height of aerial shoots ±SE (cm)	18.24±0.55	5.17±0.12	40.25±6.42	4.50±0.31	10.42±0.29	6.88±0.51
Maximum height of aerial shoots (cm)	26	7	72	6	13	10
Patch diameter (m)	>10	>5	<10	>10	>10	<3
Main depth of BGB (cm)	20	20	25	25	25	25
Maximum diameter of underground woody organs (cm)	>10	>10	7	>10	5	2.5
Depth of maximum fine root development (cm)	0–10	0–10	0–10	0–10	0–10	0–10
Presence of adventitious roots	Yes	Yes	Yes	Yes	yes	Yes

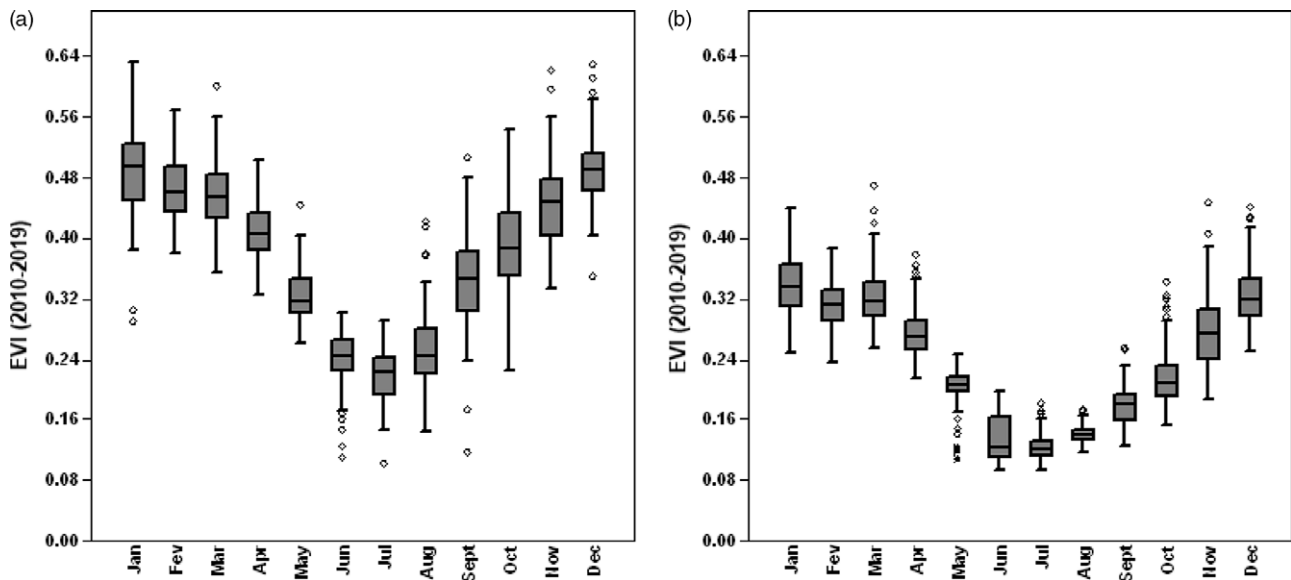*According to the classification by Pausas *et al.* 2018.

Figure 2. Annual phenology of *Brachystegia-* (a) and *Parinari-* (b) grasslands in the Cusseque study site on the Angolan central plateau. The graph shows monthly mean EVI values of a 10-year observation period (2010–2019) for 20 systematically selected sample plots. Data were derived from the combined MYD13Q1 and MOD13Q1 data products via Google Earth Engine.

grasslands starts early in April peaking in May, while in the *Brachystegia* grasslands, the fire season starts slowly in May followed by a pronounced peak much later in July (Figure 5).

Some geoxyle species (e.g. *Syzygium guineense, Landolphia gossweileri* [Stapf] Pichon, *Anisophyllea fruticulosa* Engl. and Gilg. and *Parinari capensis*) are sources of edible fruits and medicines. During the rainy season, fruits are harvested in suffrutex grasslands and eaten by the local population or sold along the main roads (e.g. Chitembro-Mumbué). Moreover, many leaves, roots and rhizomes of grassland plants are used as medicine (Firmino 2016).

At present, only very small parts of the suffrutex grasslands are used for subsistence agriculture; where this is the case, the *Parinari* grasslands are preferred for cultivation as working the soils of the *Brachystegia* grasslands without machinery is almost impossible.

Figure 3. The six geoxyle species are discussed in the text, in which four of them with topsoil are removed to show the complex woody rhizome belowground. (a) *Brachystegia russelliae*; (b) *Cryptosepalum exfoliatum* subsp. *suffruticans*; (c) *Syzygium guineense* subsp. *huillense*; (d) *Parinari capensis*; (e) *Pygmaeothamnus zeyheri*; (f) *Ochna arenaria*.
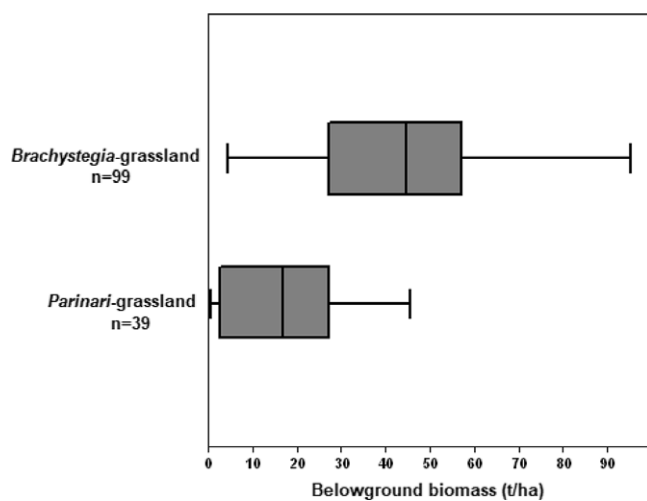

Figure 4. Box–Whisker plots showing the range of BGB in *Brachystegia russelliae*- and *Parinari capensis* grasslands.
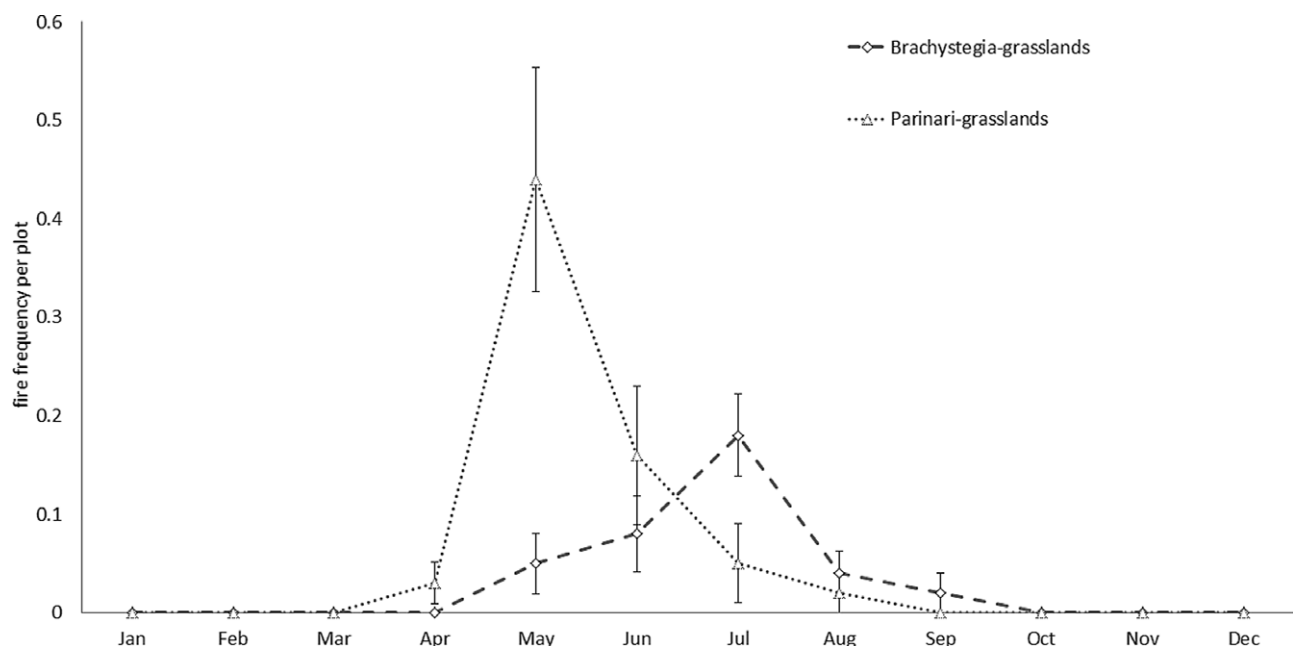
Discussion

Seasonal vegetation dynamics

Our results show strong seasonal changes of EVI in geoxylic grassland ecosystems with minima in the dry season and maxima during the peak of the rainy season. In so far, the EVI seems to follow seasonal patterns of aridity. However, a closer analysis of the data reveals that the EVI is rising already from mid-August onwards, more than 6 weeks before the onset of the rainy season in the first half of October. The period of 6–8 weeks of pre-rain green-up of suffrutex grasslands is in line with the phenological strategy of 53 +/− 18 days reported by Ryan *et al.* (2017) for wet miombo. Thus, in terms of phenology suffrutex, grasslands closely resemble the neighbouring woodland and forest ecosystems.

The parallel EVI curves of *Parinari*- and *Brachystegia* grasslands indicate constant differences in AGB and land cover between the two geoxylic grassland types throughout the year, with *Brachystegia* grasslands having significantly higher values than *Parinari* grasslands. Thus, the differences in EVI between the two grassland types are in line with the differences in BGB.

Table 2. One-way ANOVA comparing mean soil properties in two types of grassland. Significant differences are marked in bold

	Parinari grassland		*Brachystegia* grassland		One-way ANOVA	
	Mean	SE	Mean	SE	F	p(same)
Clay (%)	2.90	0.69	5.56	1.15	3.05	0.085
Silt (%)	4.72	0.72	6.26	0.49	3.37	0.071
Sand (%)	92.33	1.00	84.58	1.93	**9.59**	**0.003**
pH (H_2O)	4.82	0.08	4.76	0.06	0.33	0.566
pH (KCl)	4.32	0.05	4.18	0.05	**4.18**	**0.045**
pH (Ca_2Cl)	4.10	0.04	4.28	0.04	**7.95**	**0.006**
K (cmolc dm^{-3})	2.50	0.55	6.63	0.78	**15.55**	**0.000**
Ca (cmolc dm^{-3})	1.83	0.78	7.07	1.95	**4.62**	**0.035**
Mg (cmolc dm^{-3})	1.05	0.41	1.94	0.54	1.46	0.231
P (mg dm^{-3})	2.42	0.33	5.75	0.45	**29.15**	**0.000**
Al (cmolc dm^{-3})	0.50	0.05	0.53	0.04	0.10	0.749
Al+H (cmolc dm^{-3})	1.42	0.28	2.33	0.27	**5.07**	**0.028**
CEC (cmolc dm^{-3})	7.65	1.40	18.71	2.00	**16.67**	**0.000**
EB (cmolc dm^{-3})	5.99	1.22	15.85	2.03	**13.49**	**0.000**
V%	71.06	4.57	77.83	2.53	1.96	0.167
m%	22.17	2.53	28.94	4.57	1.96	0.167

Figure 5. Monthly number of fires per plot (mean +/− SE) over the 10-year period from 2010 to 2019 for *Parinari capensis*- and *Brachystegia russelliae* grasslands in the study area (10 sample sites per vegetation type, based on the MODIS MCD64A1 Burned Area data product).

Structure and morphology of complex belowground organs

Our results show that geoxyles have a highly complex system of underground organs, their functional origins (stem, root or tubers) being difficult to determine based on morphological observations. Anatomical analyses are needed to describe precisely the complex morpho-anatomical system of the geoxyles, as shown by Vilhalva

and Appezato da Glória (2006) who described geoxyle species occurring in the Brazilian cerrado biome.

Basal and or BBB (Clarke *et al.* 2013, Pausas *et al.* 2018) are found in all studied geoxyle species. Buds positioned below ground level are protected by the soil against short-lasting temperature extremes due to the low thermal conductivity of soils (Clarke *et al.* 2013). Thus, they allow for rapid resprouting of aerial shoots

Table 3. Global compilation of data on BGB for different vegetation types

BGB (t/ha)	Vegetation type	Country	Reference
16.0–37.0	Grassland	Czech Republic	Fiala 2011
44.6–49.4*	Grassland	USA	Fiala 2011
7.0–13.0*	Savanna	Cuba	Fiala 2011
32.0[+]	Gallery forest	Repub. of Congo	Ekoungoulou et al. 2014
44	Woodland (Old-growth Miombo)	Zambia	Chidumayo 2013
18	Woodland (Regrowth Miombo)	Zambia	Chidumayo 2013
1.2–206.3	Upland forest	Global data	Cairns et al. 1997
7.0–52.0[+]	Savanna	Global data	Grace et al. 2006
1.1–17.0	Woodland (Miombo)	Mozambique	Ryan et al. 2011
16.3–52.9	Savanna/woodland (Brazilian cerrado)	Brazil	De Castro & Kauffmann 1998
16.8	Grasslands	Brazil	Miranda et al. 2014
33.6	Shrublands	Brazil	Miranda et al. 2014
17.8	Forestlands	Brazil	Miranda et al. 2014
6–7	Wet grasslands	Brazil	Fidelis et al. 2013
16.9–43.5	Rangeland	Nepal	Limbu & Koirala 2011

*Data are included as dead BGB; [+]Modelled data.

after fire and frost, the two main local disturbances (Finckh *et al.* 2016, Revermann and Finckh 2013) and thus for the persistence of these species in the ecosystem (Pausas *et al.* 2018). Woody rhizomes are a characteristic feature amongst the dominant geoxyles of both grassland types, indicating their strong ability for vegetative, horizontal growth and lead to a competitive advantage.

Belowground biomass and carbon stock

This study is amongst the first to quantify BGB of geoxyle-dominated ecosystems in Africa. Our results show that an enormous amount of biomass is stored underground in these treeless vegetation types: *Parinari* grasslands showed an average of 16.61 t/ha BGB; in *Brachystegia* grasslands, BGB with 44.25 t/ha was significantly higher. Thus, structurally similar but floristically different suffrutex grasslands differ widely in their BGB.

BGB decreased quickly with depth and was mostly concentrated in the upper soil horizons (0–30 cm). These results concur with other results from tropical savannas, where more than 70% of BGB are reported to occur in the upper 30 cm of the soil (Jackson *et al.* 1996; de Castro & Kauffman 1998). Differences in BGB between *Parinari*- and *Brachystegia* grasslands can be attributed to the differences in the morphology of the woody underground organs, depending again on species-specific traits of the dominant geoxyle species.

Empirical studies around the globe of different vegetation types show BGB values to range from 1.1 t/ha (minimum in miombo woodland) to 206.3 t/ha (maximum in Douglas fir forests) (Table 3). The BGB recorded for the suffrutex grasslands in central Angola amount to similar values recorded in other grassland and tropical savanna ecosystems (Table 3). As such, they are also in the range reported by De Castro & Kauffmann (1998) for the Brazilian cerrado, another geoxyle-rich ecosystem.

Comparing the obtained BGB values for the two types of suffrutex grasslands with regional studies on woodland vegetation

shows that BGB in *Parinari* grasslands is at least as high and that *Brachystegia* grasslands partly even exceed these values: Ryan *et al.* (2011) recorded 17.2 t/ha in miombo woodlands in Mozambique and Chidumayo (2013) estimated 18 t/ha and 44 t/ha (for regrowth and old-growth, respectively) in Zambian miombo woodlands. The relevance of the BGB of suffrutex grasslands is further illustrated by a comparison of our measured BGB data with AGB estimates of the surrounding miombo woodlands. Sichone *et al.* (2018) report, depending on the allometric equation used, a median of 48.8 or 60.4 t/ha AGB for the miombo woodlands on the Angolan Central Plateau. Accordingly, the BGB of the geoxylic *Brachystegia* grasslands almost equals the amount of AGB of the neighbouring woodlands.

According to the land cover classification of Schneibel *et al.* (2013), *Brachystegia* grasslands cover about 23.3% of the study site and *Parinari* grassland a further 8.5% ,and thus cover a substantial share of the land surface on the Angolan Central Plateau (and further parts of the miombo region).

Although the AGB component of suffrutex grasslands is negligible (branches of most geoxyle species barely reach a few decimetres in height), these figures highlight the relevance of taking suffrutex grasslands into account for carbon stock assessments in the miombo region and also for African savannas if geoxyles form an important part of the vegetation. Especially for remote sensing-based studies, it should be highlighted that BGB of structurally similar vegetation types, in this case, *Brachystegia* and *Parinari* grasslands, can differ fundamentally in their BGB allocation.

Soil properties and physiological reasons for high BGB allocation

Many factors are thought to influence BGB allocation. Soil characteristics such as nutrient availability (Cavelier 1992, Gower 1987, Pérez-Harguindeguy *et al.* 2013) and texture (Keyes and Grier

1981, Vitousek and Sanford Jr. 1986, Vogt *et al.* 1995, Waring and Schlesinger 1985) were reported to have a significant influence on root biomass allocation.

As shown by our analyses, the soils of the study region are dystrophic or nutrient-poor soils common in tropical regions (Ronquim 2010) and characteristic of the miombo belt (Frost 1996). Soil properties did not vary considerably in our study area. However, some of the significant differences in soil properties between the two geoxylic grassland types (sand content, pH [in KCl and CaCl₂], K, Ca, P, Al+H, CEC, SB, V% and m%) reflect differences due to parent material, landform and topographic position in the landscape, which also affect water permeability, soil moisture and transport of ions within soils and could explain the differences in species composition, BGB and carbon stocks between the two types of grasslands.

The absence of sodium in almost all analysed soil samples can be explained by its great solubility. Under conditions of high rainfall and coarse sandy texture in inclined landscapes, sodium is rapidly leached from the soil profile (Duchaufour 1982). The climate of our study area is sufficiently humid and the drainage of the sandy soils is good enough to rapidly remove soluble cations like sodium from the soil profile.

The results of the soil analyses are in line with Gröngröft *et al.* (2013). Extreme soil conditions, associated with an intense local disturbance regime (fire and frost) appear to be contributing to high BGB allocation. As well as the main miombo species, geoxyles have developed adaptations to survive in nutrient-poor habitats, withdrawing nutrients before leaf shedding at the onset of the cold dry season and storing them in belowground organs for later use (Aerts and van der Peijl 1993). This seems to be one of the main strategies used to cope with low soil nutrient availability. Leaf analysis of the main species from suffrutex grasslands at the Cusseque area revealed normal nutrient contents, not reflecting the low nutrient availability in soils (Gomes *et al.* 2019). Differences in biomass allocation (BGB vs. AGB) between woodlands and suffrutex grasslands in miombo suggest that geoxyles invest more in belowground structures as an adaptation to cope with the high disturbance regime aboveground (e.g. frost and fire) (Finckh *et al.* 2016, Maurin *et al.* 2014).

Human impacts on suffrutex grasslands

So far, the low interest in agricultural use of the suffrutex grasslands has maintained these ecosystems and their stunning species diversity. With few exceptions, suffrutex grasslands in the study area were little impacted by human activities.

The only notable exception is man-made fire. Natural ignition is virtually absent during the grassland fire season, and thus almost all fires can be attributed to human activities (Stellmes *et al.* 2013b). It is important to highlight the difference in fire seasonality between the two structurally similar geoxylic grassland types as they have important management implications for handling and for the prevention of fires. Due to the denser vegetation and higher share of geoxyles in the vegetation cover, the *Brachystegia* grasslands retain higher humidity in the dry season and thus early dry season burning is reduced (M. Finckh, unpublished experimental data). However, in terms of late dry season fires (which imply a much higher risk to affect the adjacent dense miombo woodlands), the two grassland types do not differ significantly.

In both vegetation types, fires remove dry AGB of grasses and geoxyles and leave the landscape widely bare for a short period of time. However, geoxyles and also the associated grass and forb

species are well adapted to this disturbance regime. The removal of AGB by fire may be an important factor leading to vegetative and reproductive renewal (Bond *et al.* 2005). We noted that local people also use fire to manage or enhance the production of some of the wild edible fruits that grow in these grasslands.

The currently still widely natural state of the geoxyle-dominated ecosystems on the Angolan Central Plateau may, however, be strongly affected by the increasing availability of agricultural machinery and turn the *Brachystegia* grasslands into targets for agro-industrial transformation. This would lead to great losses of BGB and the corresponding release of the current carbon stocks into the atmosphere. Misdirected afforestation attempts may cause similar destructive consequences to these fascinating ecosystems and their associated flora and fauna (Veldman *et al.* 2019).

Conclusion

The study revealed for the first time, based on empirical data, the high relevance of BGB stored in the 'Underground Forests of Africa', grasslands dominated by geoxyles that occur throughout south-central Africa. We reported data from the Angolan Central Plateau that show that belowground carbon stocks in these ecosystems are much higher than in neighbouring miombo woodlands and, in the case of *Brachystegia* grasslands, are almost as high as values for aboveground carbon stocks in the surrounding woodlands. Thus, any study on regional and global carbon stock assessments need to take these findings into account. Furthermore, we provided insights into the morphology, structure and environmental drivers leading to the success of the geoxylic life form. Currently, suffrutex grasslands are, due to their low soil fertility and the extended root network, largely excluded from agriculture cultivation. The advent of agro-industrial machinery may, however, change this situation rapidly.

References

Aerts R and van der Peijl MJ (1993) A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. *Oikos* **66**, 144–147. https://doi.org/10.2307/3545208.

Bond WJ, Woodward FI and Midgley GF (2005) The global distribution of ecosystems in a world without fire. *New Phytologist* **165**, 525–538. https://doi.org/10.1111/j.1469-8137.2004.01252.x

Cairns MA, Brown S, Helmer EH and Baumgardner GA (1997) Root Biomass Allocation in the World's Upland Forests. *Oecologia* **111**, 1–11. https://doi.org/10.1007/s004420050201.

Cavelier J (1992) Fine-root biomass and soil properties in a semideciduous and a lower montane rain forest in Panama. *Plant and Soil* **142**, 187–201. https://doi.org/10.1007/BF00010965.

Chamberlain JL, Ness G, Small CJ, Bonner SJ and Hiebert EB (2013) Modelling belowground biomass to improve sustainable management of Actaea racemosa, a globally important medicinal forest product. *Forest Ecology and Management* **293**, 1–8. https://doi.org/10.1016/j.foreco.2012.12.042.

Chidumayo EN (2013) Estimating tree biomass and changes in root biomass following clear-cutting of Brachystegia-Julbernardia (miombo) woodland in central Zambia. *Environmental Conservation* **41**, 54–63. https://doi.org/10.1017/S0376892913000210.

Ciais P, Bombelli A, Williams M, Piao SL, Chave J, Ryan CM, Henry M, Brender P and Valentini R (2011) The carbon balance of Africa: synthesis of recent research studies. *Philosophical Transactions of The Royal Society A Mathematical Physical and Engineering Sciences* **369**, 2038–2057. https://doi.org/ 10.1098/rsta.2010.0328.

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ and Knox KJE (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* **197**, 19–35. https://doi.org/ 10.1111/nph.12001.

Coupland RT (1992) *Mixed prairie*. In Coupland RT (Ed), *Grasslands of the World*. Cambridge: Cambridge University Press, pp. 151–182.

de Castro EA and Kauffman JB (1998) Ecosystem structure in the Brazilian Cerrado : A vegetation gradient of aboveground biomass, root mass and consumption by fire. *Journal of Tropical Ecology* **14**, 263–283. https://doi.org/10.1017/S0266467498000212.

Dengler J (2009) A flexible multi-scale approach for standardised recording of plant species richness patterns. *Ecological Indicators* **6**, 1169–1178. https://doi.org/10.1016/j.ecolind.2009.02.002.

du Rietz GE (1931) Life-forms of terrestrial flowering plants. *Acta Phytogeographica Suecica* **3**, 1–95.

Duchaufour P (1982) *Pedology, Pedogenesis and Classification*, 1st ed. London: George Allen & Unwin (Publishers) Ltd.

Ekoungoulou R, Liu X, Loumeto JJ and Ifo SA (2014) Tree Above-and Belowground Biomass Allometries for Carbon Stocks Estimation in Secondary Forest of Congo. *Journal of Environmental Science, Toxicology and Food Technology* **8**, 9–20. https://doi.org/10.9790/2402-08420920

Fiala K (2011) Belowground plant biomass of grassland ecosystem and its variation according to ecological factors. *Ekológia* **29**, 206–210. https://doi.org/10.4149/ekol.

Fick S and Hijmans R (2017) WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**. https://doi.org/10.1002/joc.5086.

Fidelis A, Lyra MFS and Pivello V (2013) Above- and belowground biomass and carbon dynamics in Brazilian Cerrado wet grasslands. *Journal of Vegetation Science* **24**, 356–364.

Finckh M, Revermann R and Aidar MPM (2016) Climate refugees going underground – a response to Maurin et al. (2014). *New Phytologist* **209**, 904–909. https://doi.org/ 10.1111/nph.13567.

Firmino RKVS (2016) *Valorização da flora de Cusseque e Caiundo no centro e sul de Angola e avaliação da biomassa lenhosa utilizada para combustível e construção*. Potugal: Universidade de Lisboa.

Frost P (1996) *The ecology of miombo woodlands*. In Campbell B (Ed.), *The Miombo in Transition: Woodlands and Welfare in Africa*. Bogor: Centre for International Forestry Research, pp. 11–57.

Gomes AL, Revermann R, Gonçalves FMP, Lages F, Aidar MPM, Finckh M and Jürgens N (2019) Tree or not tree: Differences in plant functional traits among geoxyles and related trees species. *South African Journal of Botany* **127**, 176–184. https://doi.org/10.1016/j.sajb.2019.08.044.

Gower ST (1987) Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests: a hypothesis. *Biotropica* **19**, 171–175. https://doi.org/10.2307/2388741.

Grace J, San José J, Meir P, Miranda HS and Montes RA (2006) Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography* **33**, 387–400. https://doi.org/10.1111/j.1365-2699.2005.01448.x

Gröngröft A, Luther-Mosebach J, Landschreiber L and Eschenbach A (2013) Cusseque - Soils. *Biodiversity & Ecology* **5**, 51–54. https://doi.org/10.7809/b-e.00245.51

IPCC (2006) 2006 IPCC Guidelines for National Greenhouse Gas Inventories, IPCC National Greenhouse Gas Inventories Programme. Institute for Global Environ-mental Strategies, Tokyo. Institute for Global Environmental Strategies, Kanagawa.

Jackson RB, Canadell J, Ehlinger JR, Mooney HA, Sala OE and Schulze, ED (1996) A global analysis of root distribution for terrestrial biomes. *Oecologia* **3**, 389–411. https://doi.org/10.1007/BF00333714.

Keyes MR and Grier CC (1981) Above- and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forestry Research* **11**, 599–605. https://doi.org/10.1139/x81-082

Kolbek J and Alves RJV (2008) Impacts of cattle, fire and wind in rocky savannas, southeastern Brazil. *Acta Universitatis Carolinae – Environmentalica* **22**, 111–130.

Lichacz W, Hardiman S and Buckney RT (2009) Wetlands (Australia), 2009 [WWW Document]. URL ojs.library.unsw.edu.au.

Limbu DK and Koirala M (2011) Above-ground and belowground biomass situation of Milke-Jaljale Rangeland at different altitudinal gradient. *Our Nature* **9**, 107–111. https://doi.org/10.3126/on.v9i1.5740.

Lindman CAM (1914) Några bidrag till frågan: buske eller träd? Särtryck sidan 231-287 i K. Vetenskapsakademiens årsbok Årg. Uppsala.

Maurin O, Davies TJ, Burrows JE, Daru BH, Yessoufou K, Muasya AM, van der Bank M and Bond WJ (2014) Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist* **204**, 201–214. https://doi.org/10.1111/nph.12936.

Miranda SC, Bustamante M, Palace M, Hagen S, Keller M and Ferreira LG (2014) Regional Variations in biomass distribution in Brazilian savanna woodland. *Biotropica* **46**, 125–138. https://doi.org/10.1111/btp.12095

Mokany K Raison RJ and Prokushkin AS (2006) Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biology* **1**, 84–96. https://doi.org/10.1111/j.1365-2486.2005.001043.x

Nabuurs GJ, Ravindranath NH, Paustian K, Freibauer A, Hohenstein W and Makundi W (2003) *Forest land*. In Penman J, Gytarsky M, Hiraishi T, Krug T, Kruger D, Pipatti R, Buendia L, Miwa K, Ngara T, Tanabe K and Wagner F (eds), *Good Practice Guidance for Land Use, Land Use Change and Forestry*. Kanagawa: Institute for Global Environmental Strategies. https://doi.org/citeulike-article-id:1260638.

Nieto-Quintano P, Edward TAM, Rolando O, Marcele ABM, Tim R and Casey MR (2018) The mesic savannas of the Bateke Plateau: carbon stocks and floristic composition. *Biotropica*, 1–13. https://doi.org/10.1111/btp.12606.

Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B and Fidelis A (2018) Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist* **217**, 1435–1448. https://doi.org/10.1111/nph.14982.

Pérez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, Vos,AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, Steege H, Heijden MGA, van der Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S and Cornelissen JHC (2013) New Handbook for standardized measurment of plant functional traits worldwide. *Australiam Journal of Botany* **61**, 167–234. https://doi.org/10.1071/BT12225.

Ravindranath NH and Ostwald M (2008) *Carbon Inventory Methods: Handbook for Greenhouse Gas Inventory, Carbon Mitigation and Roundwood Production Projects*. Springer. https://doi.org/10.1007/978-1-4020-6547-7.

Reverman R, Gonçalves FMP, Gomes AL and Finckh M (2017) Woody species of the miombo woodlands and geoxylic grasslands of the Cusseque area, south-central Angola. *Checklist* **13**, 1–10.

Revermann R and Finckh M (2013) Cusseque - Microclimate. *Biodiversity & Ecology* **5**, 47–50. https://doi.org/10.7809/b-e.00244.47.

Revermann R, Gonçalves FM, Gomes AL and Finckh M (2013) Cusseque - Vegetation. *Biodiversity & Ecology* **5**, 59–63. https://doi.org/10.7809/b-e.00247.59.

Revermann R, Oldeland J, Gonçalves FM, Luther-Mosebach J, Gomes AL, Jürgens N and Finckh M (2018) Dry tropical forests and woodlands of the Cubango Basin in southern Africa - first classification and assessment of their woody species diversity. *Phytocoenologia* **48**, 23–50. https://doi.org/10.1127/phyto/2017/0154.

Robertson F (2005) Ecological processes within the four corners area. Occasional Publications in Biodiversity, Bulawayo. www.biodiversity foundation.org.

Ronquim CC (2010) Conceitos de fertilidade do solo e manejo adequado para as regiões tropicais. *Boletim de Pesquisa e Desenvolvimento* **8**, 26.

Rosillo-Calle F, de Groot P, Hemstock S, Woods J (2007) *The biomass assessment handbook, bioenergy for a sustainable environment*. London: EARTHSCAN.

Ryan CM, Williams M and Grace J (2010) Above- and belowground carbon stocks in a Miombo wooodland landscape of Mozambique. *Biotropica* **43**, 423–432. https://doi.org/10.1111.j.1744-7429.2010.00713.x.

Ryan CM, Williams M, Grace J, Woollen E and Lehmann CER (2017) Pre-rain green-up is ubiquitous across southern tropical Africa: implications for temporal niche separation and model representation. *New Phytologist* **213**, 625–633. https://doi.org/ 10.1111/nph.14262

Sanford RLJ and Cuevas E (1996) *Root growth and rhizosphere interactions in tropical forests*. In Mulkey SS, Chazdon RL and Smith AP (eds), *Tropical Forest Plant Ecophysiology*. New York: Chapman and Hall, pp. 268–300.

Schlesinger WH (1997) *Biogeochemistry, an analysis of global change*. New York: Academic Press.

Schneibel A, Stellmes M, Frantz D, Finckh M and Revermann R (2013) Cusseque – Earth Observation. In Oldeland J, Erb C, Finckh M and Jürgens N (eds), Environmental assessments in the Okavango Region. Biodiversity & Ecology 5, 55–57.

Sichone P, De Cauwer V, Chissingui AV, Gonçalves FMP, Finckh M, Revermann R (2018) *Patterns of above-ground biomass and its environmental drivers: an analysis based on plot based surveys in the dry tropical forests and woodlands of southern Africa*. In Revermann R, Krewenka KM, Schmiedel U, Olwoch JM, Helmschrot J & Jürgens N (eds), *Climate change and adaptive land management in southern Africa – assessments, changes, challenges, and solutions, Biodiversity & Ecology*. 6, Göttingen & Windhoek: KlausHess Publishers, pp. 309–316. https://doi.org/10.7809/b-e.00338.

Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT and Hughes CE (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *PNAS* **106**, 20359–23064. https://doi.org/10.1073/pnas.0903410106.

Stellmes M, Frantz D, Finckh M and Revermann R (2013a) Fire frequency, fire seasonality and fire intensity within the Okavango region derived from MODIS fire products. *Biodiversity & Ecology* **5**, 351–362. doi: 10.7809/b-e.00288.

Stellmes M, Frantz D, Finckh M and Revermann R (2013b) Okavango Basin-Earth Observation. *Biodiversity & Ecology* **5**, 23–28. https://doi.org/10.7809/b-e.00239.

Veldman JW, Aleman JC, Alvarado ST, Anderson TM, Archibald S, Bond WJ, Boutton TW, Buchmann N, Buisson E, Canadell JG, Dechoum MS, Diaz-Toribio MH, Durigan G, Ewel JJ, Fernandes GW, Fidelis A, Fleischman F, Good SP, Griffith DM, Hermann J-M, Hoffmann WA, Le Stradic S, Lehmann CER, Mahy G, Nerlekar AN, Nippert JB, Noss RF, Osborne CP, Overbeck GE, Parr CL, Pausas JG, Pennington RT, Perring MP, Putz FE, Ratnam J, Sankaran M, Schmidt IB, Schmitt CB, Fernando AO, Silveira FAO, Staver AC, Stevens N, Still CJ, Strömberg CAE, Temperton VM, Varner JM and Zaloumis NP (2019) Comment on "The global tree restoration potential". *Science* https://doi.org/10.1126/science.aay7976

Vilhalva DAA and Appezzato-da-Gloria B (2006) Belowground morpho-anatomy system of *Calea verticillata* (Klatt) Pruski and *Isostigma megapotamicum* (Spreng.) Sherff – Asteraceae. *Brazilian Journal of Botany* **26**, 39–47. https://doi.org/10.1590/S0100-84042006000100005.

Vitousek PM and Sanford Jr, RL (1986) Nutrient Cycling in Moist Tropical Forest. *Annual Review of Ecology, Evolution and Systematics* **17**, 137–167. https://doi.org/10.1146/annurev.ecolsys.17.1.137

Vogt KA, Vogt DJ, Brown S, Tilley JP, Edmonds RL, Silver WL and Siccama TG (1995) *Dynamics of forest floor and soil organic matter accumulation in boreal, temperate, and tropical forests*. In Lal R, Kimble J, Levine E and Stewart BA (eds), *Soil Management and Greenhouse Effect*. Florida USA: CRC Lewis Publishers, pp. 159–178.

Waring RH and Schlesinger WH (1985) *Forest ecosystems: concepts and management*. Orlando: Academic Press.

Weber T (2013) Cusseque climate. *Biodiversity & Ecology* **5**, 45–46. https://doi.org/10.7809/b-e.00243.

Wetzel RG and Howe MJ (1999) High production in a herbaceous perennial plant achieved by continuous growth and synchronized population dynamics. *Aquatic Botany* **64**, 111–129. https://doi.org/10.1016/S0304-3770(99)00013-3.

White F (1976) The underground forests of Africa : a preliminary review. *Gardens's Bulletin Singapore* **29**, 57–71. https://biostor.org/reference/134550.

Zigelski, P, Gomes, A and Finckh, M (2019). *Suffrutex Dominated Ecosystems*. In Huntley BJ, Russo V, Lages F and Ferrand N (eds), *Biodiversity of Angola; Science and Conservation: A Modern Synthesis*. Cham, Switzerland: Springer, pp. 109–119.