HOW ROOT MORPHOLOGY AND FUNCTIONAL TRAITS ENABLE GEOXYLES TO THRIVE IN NUTRIENT POOR AND DISTURBANCE PRONE ANGOLAN MIOMBO ECOSYSTEMS

Dissertation

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Contents

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To increase the readability of the thesis, all figures, tables and supporting information have been renumbered in a consecutive manner and the references are listed alphabetically at the end. Moreover, a single combined reference section is provided and one section containing all supporting information is given at the end of the thesis. The terminology for geoxylic suffrutices was changed throughout to geoxyles. An identification error has been corrected in paper 1.

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Resumo

O ecossistema de miombo domina cerca de 47% do território de Angola, especialmente na parte central do país. Faz parte da grande ecorregião do miombo, que se estende desde a Escarpa Angolana até ao Oceano Índico em Moçambique e na Tanzânia, cobrindo mais de 3,8 milhões de km².

Em geral, as matas de miombo formam um mosaico com pastagens co-dominadas por arbustos geoxílicos (geoxylic suffrutices ou geoxyles). Geoxyles são arbustos rasteiros ou subarbustos com caules aéreos de vida curta, mas com enorme desenvolvimento de caules, raízes e ramos lenhosos subterrâneos. As geoxyles têm o seu centro de diversidade global no fitocório da Zâmbia, onde ocorrem em mais de 30 famílias diferentes.

Como os campos geoxyles são um ecossistema importante e pouco estudado do ecossistema de miombo, realizei estudos sobre diversidade, morfologia das raízes, características funcionais (PFTs) e funções ecológicas das geoxyles na parte sul do Planalto do Bié (município de Chitembo, centro-sul de Angola) como parte do projecto The Future Okavango (TFO). Os objectivos foram: a) fornecer uma visão geral actualizada da diversidade e distribuição de geoxyles e das pastagens co-dominadas por geoxyles em Angola; b) descrever a dinâmica da vegetação, arquitetura de raízes, biomassa de madeira e propriedades do solo das pastagens de geoxyles; c) estudar o papel de características funcionais (PFTs) de geoxyles em comparações com os seus pares arbóreos estreitamente relacionadas e d) ver se as características funcionais (PFTs) de certos grupos filogenéticos diferem e podem ajudar-nos a explicar a dominância das Fabaceae-Detarioideae nos ecossistemas de miombo.

Uma visão geral dos ecossistemas dominados por geoxyles em Angola, informações sobre a sua exploração científica inicial, a sua distribuição, biodiversidade e endemismos são fornecidos na primeira parte da minha dissertação (Capítulo 2).

Com base nas nossas observações e dados de campo, bem como na literatura existente, forneço ao leitor informações detalhadas sobre a importância das pastagens de geoxyles e enfatizo a necessidade de proteger esses ecossistemas especiais, que foram cientificamente pouco explorados até agora. Identifiquei as acções antrópicas que ameaçam esses ecossistemas, em particular o desenvolvimento da agricultura nessas áreas.

Uma característica marcante das geoxyles é o fraco desenvolvimento das suas partes aéreas e o enorme desenvolvimento de rizomas e raízes lenhosas no solo. Esta rede lenhosa de órgãos de armazenamento subterrâneos constitui o principal reservatório de biomassa e estoque de carbono desse ecossistema, que até agora não tem sido considerado no balanço de carbono dos ecossistemas de miombo. Para ter uma ideia do seu potencial no sequestro de carbono, medi com os meus co-autores essa biomassa lenhosa abaixo do solo no meu segundo artigo (Capítulo 3) e descrevi a estrutura dos órgãos lenhosos subterrâneos de seis espécies de geoxyles dominantes (três para cada um dos dois tipos de solos que ocorrem na área de estudo). Nos solos ferralíticos, *Brachystegia russelliae*, *Cryptosepalum exfoliatum* subsp. *suffruticans* e *Syzygium guineense* subsp. *huillensis* foram seleccionados; nos solos arenosos, *Parinari capensis*, *Pygmaeothamnus zeyheri* e *Ochna arenaria*. Calculou-se e discutiu-se a biomassa subterrânea e o estoque de carbono correspondentes, cuja magnitude é comparável às florestas tropicais secas. Ambos, biomassa subterrânea e o regime de perturbação pelo fogo diferem muito entre os dois tipos de vegetação geoxílica.

Outra característica importante das pastagens de geoxyles é a existência de espécies arbóreas ou arbustivas intimamente relacionadas para cada espécie de geoxyles. No terceiro artigo descrevo e discuto em comparação as diferenças em PFTs de seis desses pares (geoxyles versus árvores) na área de estudo de Chitembo (Capítulo 4). Foram medidos e comparados, a área foliar específica (SLA), espessura da folha (LT), densidade da madeira (WD), conteúdo foliar de nitrogênio (LN), carbono (LC), fósforo (LP), potássio (LK), cálcio (LCa) e magnésio (LMg), bem como o teor de matéria seca das folhas (LDMC). Além disso, foi medido também o potencial hídrico da folha (WP) dos pares comparados durante as estações seca e chuvosa. Essas características funcionais são conhecidas por mostrarem respostas a uma ampla gama de factores ambientais e uma estreita associação com mecanismos ecofisiológicos. Os resultados deste estudo sugerem que as diferenças nas características funcionais das geoxyles e das árvores são adaptações aos estresses ambientais específicos dos seus respectivos habitats.

No quarto artigo (Capítulo 5), foram medidas e comparadas as características funcionais (PFTs) de um conjunto mais extenso de geoxyles e árvores comuns na área de estudo. Por esta razão o banco de dados foi extendido para doze geoxyles e catorze árvores. Para investigar as diferentes adaptações com as quais essas espécies lidam com as condições ambientais do seu habitat, foram analisadas e discutidas as diferenças em PFTs entre grupos filogenéticos e tipos de estratégia simbiótica (Fabaceae versus não Fabaceae; espécies ectomicorrizadas versus espécies não micorrazadas). Os resultados mostraram claramente adaptações ecofisiológicas e simbióticas que se desenvolveram em certas linhas filogenéticas durante a evolução, permitindo-as lidar eficientemente com as condições extremas do habitat. A dominância geral de Fabaceae-Detarioidae nos solos pobres em nutrientes do ecossistema de miombo parece ser fortemente influenciada por sua associação ectomicorríca e, portanto, maior capacidade de absorção de fósforo. Estudos de ecossistemas semelhantes na ecoregião do miombo seriam necessários para apoiar esta hipótese.

Finalmente, os resultados mais importantes dos quatro artigos que constituem a tese são resumidos e discutidos num capítulo de síntese (Capítulo 6).

Summary

The miombo ecoregion encompasses a vast African dry woodland ecosystem that dominates about 47% of Angola's territory, especially in the central areas of the country. The ecoregion, which extends from the Angolan escarpment to the Indian Ocean in Mozambique and Tanzania, covers more than 3.8 million km².

In general, miombo ecosystems form a mosaic of forest and woodland patches with grasslands co-dominated by geoxyles. Geoxyles (also known as geoxylic suffrutices) are low shrubs or semi-shrubs with mostly short-lived above-ground shoots but strong development of underground woody shoots, roots and tubers. Geoxyles have their global diversity centre in the Zambezian phytochorion, where geoxyles from more than 30 different plant families occur.

As grasslands dominated by geoxyles are an important and little studied part of the miombo ecoregion, I have conducted studies on diversity, root morphology, functional traits (PFTs) and ecological functions of geoxyles on the southern slope of the Bié Plateau (Chitembo municipality, south central Angola) as part of the Future Okavango (TFO) project. My objectives were a) to provide an updated overview of the diversity and distribution of geoxyles and geoxyle grasslands in Angola, b) to describe the vegetation dynamics, root architecture, wood biomass and soil properties of geoxyle grasslands, c) to study the role of functional traits (PFTs) of geoxyles in pairwise comparisons with closely related tree species, and d) to see if the functional traits (PFTs) of certain phylogenetic groups differ and can help us explain the dominance of detarioid Fabaceae in miombo ecosystems.

Chapter 1 provides a general introduction to miombo ecosystems and to geoxyle grasslands.

An overview of the ecosystems dominated by geoxyles in Angola, information on their early scientific exploration, their distribution, biodiversity and endemisms is given in the first essay of my dissertation (Chapter 2). Based on our observations and data as

well as the existing literature, I provide the reader with detailed information on the importance of geoxyle grasslands and emphasize the need to protect these special ecosystems, which have been scientifically largely unexplored so far. Together with my co-authors, I have identified the human activities that threaten these ecosystems, in particular intensive agricultural development in these areas.

A striking feature of geoxyle species is the weak development of their above-ground shoots and the comparatively very strong development of woody rhizomes, roots and tubers in the soil. This woody network of subterranean woody shoot axes and storage organs forms the main pool of biomass and carbon stocks of the geoxyle grassland ecosystems, which so far have not yet been considered in carbon balances of miombo ecosystems. To get an idea of its carbon stocks, I measured the belowground biomass pool in my second paper (Chapter 3) and described the structure of the subterranean woody organs of six dominant geoxyle species (three for each of the two soil types occurring in my study area). I selected *Brachystegia russelliae*, *Cryptosepalum exfoliatum* ssp. *suffruticans* and *Syzygium guineense* ssp. *huillense* from ferralitic areas and *Parinari capensis*, *Pygmaeothamnus zeyheri* and *Ochna arenaria* from sandy sites. I calculated and discussed the subterranean biomass and the corresponding carbon stock, whose magnitude is comparable to dry tropical forests. Both, biomass and the disturbance regime by fire differ greatly between the two geoxyle vegetation types.

Another important feature of geoxyle grasslands is the existence of phylogeneticaly related tree or shrub species for each geoxyle species. My third paper describes and discusses the differences in PFTs of six of these congeneric pairs (geoxyles versus trees) in the Chitembo study area (Chapter 4). Together with my co-authors, I measured and compared specific leaf area (SLA), leaf thickness (LT), wood density (WD), leaf contents of nitrogen (LN), carbon (LC), phosphorus (LP), potassium (LK), calcium (LCa) and magnesium (LMg) as well as leaf dry matter content (LDMC). Additionally, we measured the leaf water potential (WP) of the compared pairs during the dry and rainy season. These traits are known to show responses to a wide range of environmental factors and a close association with ecophysiological mechanisms. The results of this study suggest that differences in functional characteristics of geoxyles and trees are adaptations to the specific environmental stresses of their respective habitats.

In my fourth paper (Chapter 5) I measure and compare the functional traits (PFTs) of an extended set of geoxyle and tree species which occur frequently in my study area. For this purpose the database was extended to twelve geoxyles and fourteen trees. To investigate the different adaptations with which these species cope with the environmental conditions of their habitat, I analysed and discussed differences in PFTs between phylogenetic groups and symbiotic strategy types (Fabaceae versus non-Fabaceae; Ectomycorrhiza associated versus non-mycorrhizal species). The results clearly show ecophysiological and symbiotic adaptations that developed in certain phylogenetic lines during evolution, enabling them to successfully cope with extreme habitat conditions. The general dominance of detarioid Fabaceae on the nutrient-poor soils of the miombo belt seems to be strongly influenced by their ectomycorrhiza association and thus superior phosphorus uptake capacity. Studies from comparable ecosystems of the miombo ecoregion would be required to support this hypothesis.

Finally, I summarise and discuss the most important results of my four papers in a synthesis chapter (Chapter 6).

Zusammenfassung

Miombo-Ökosysteme dominieren ungefähr 47 % des angolanischen Staatsgebiets, besonders in den zentralen Bereichen des Landes. Sie sind Teil der größeren Miombo Ökoregion, die sich mit mehr als 3,8 Mio km² vom westlichen angolanischen Escarpment bis an die Küste des indischen Ozeans in Mozambique und Tanzania erstreckt.

Im Allgemeinen bilden Miombo-Wälder ein Mosaik mit Grasländern, die von geoxylen Halbsträuchern (geoxylic suffrutices oder geoxyles) co-dominiert werden. Geoxyle Halbsträucher sind niedrige Sträucher oder Halbsträucher mit meist nur kurzlebigen oberirdischen Sprossen, aber langlebigen unterirdischen holzigen Sprossachsen, Wurzeln und Knollen. Sie haben ihr globales Diversitätszentrum im zambesischen Phytochorion, wo geoxyle Halbsträucher aus mehr als 30 unterschiedlichen Pflanzenfamilien vorkommen.

Da Geoxyle-Grasländer ein wichtiges und bisher wenig erforschtes Ökosystem des Miombo-Gürtels sind, habe ich im Rahmen des Future Okavango (TFO)-Projekts Untersuchungen zu Diversität, Wurzelmorphologie, funktionellen Merkmalen (PFTs) und den ökologischen Funktionen von geoxylen Halbsträuchern am Südhang des Bié-Plateaus in Zentralangola durchgeführt. Meine Ziele waren a) einen aktualisierten Überblick über Diversität und Verbreitung von geoxylen Halbsträuchern und Geoxyle-Grasländern in Angola zu geben, b) die Vegetationsdynamik, Wurzelarchitektur, Holzbiomasse und Bodeneigenschaften von Geoxyle-Grasländern zu beschreiben, c) die Rolle funktioneller Merkmale (PFTs) von geoxylen Halbsträuchern in Paarvergleichen mit nahe verwandten Baumarten zu untersuchen und d) zu schauen, ob die funktionellen Merkmale (PFTs) bestimmter phylogenetischer Gruppen sich unterscheiden und uns helfen können, die Dominanz detarioider Fabaceen in den Miombo-Ökosystemen zu erklären.

Einen Überblick über die von geoxylen Halbsträuchern in Angola dominierten Ökosysteme, Informationen zu frühen Erkundungen, ihrer Verbreitung, Artenvielfalt und Endemismen bietet der erste Aufsatz meiner Dissertation (Kapitel 2). Basierend auf unseren Beobachtungen und Daten sowie der existierenden Literatur gebe ich (mit meinen Mitautoren) dem Leser detaillierte Informationen über die Bedeutung von Geoxyle-Grasländern und betone die Notwendigkeit, diese besonderen Ökosysteme zu schützen, die bisher wissenschaftlich weitgehend unerforscht sind. Wir haben auch Entwicklungen identifiziert, die diese Ökosysteme gefährden, insbesondere die Entwicklung intensiver Landwirtschaft in diesen Gebieten.

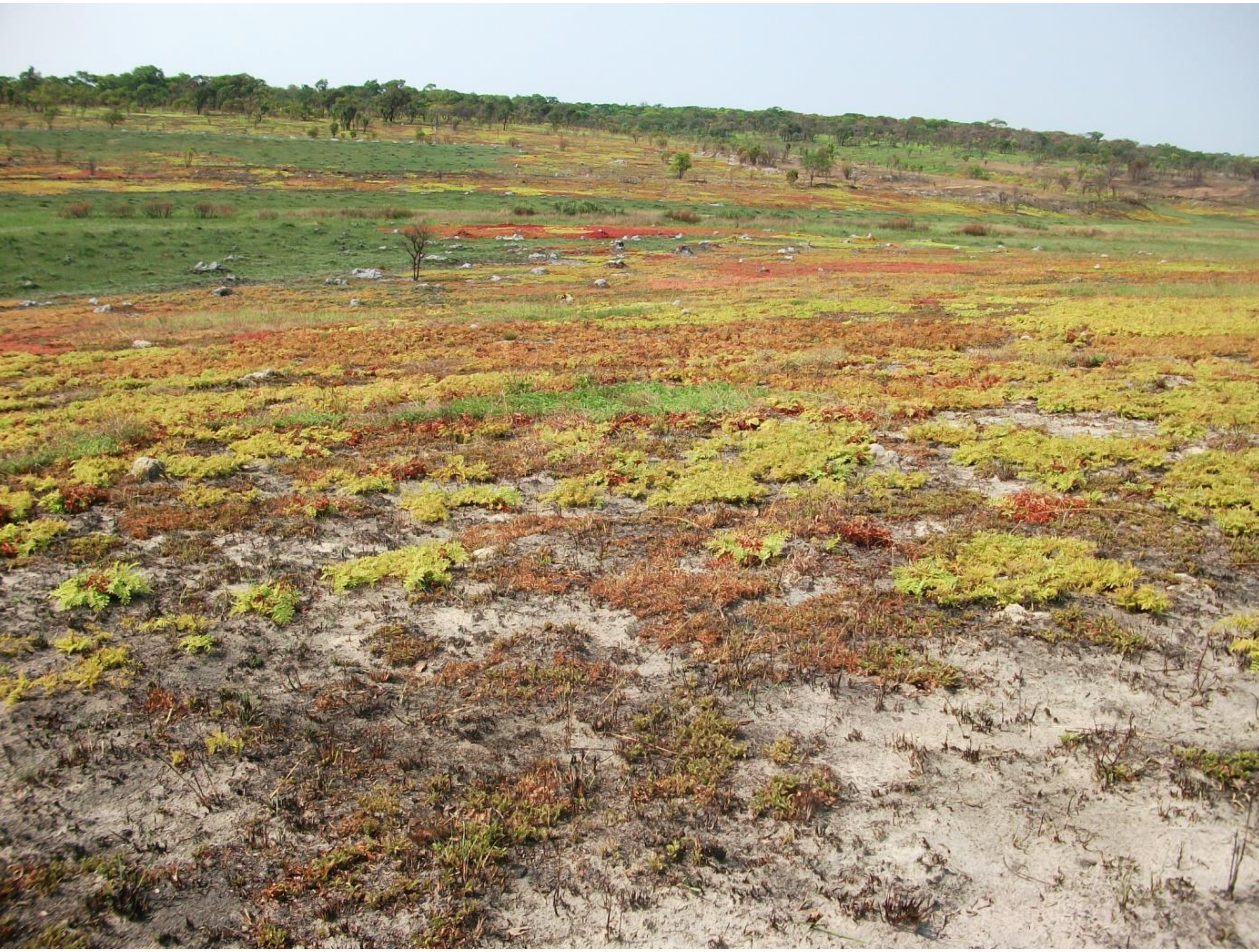
Ein auffälliges Merkmal der geoxylen Halbsträucher ist die schwache Entwicklung ihrer oberirdischen Sprosse und die vergleichsweise sehr starke Entwicklung der Rhizome, Holzwurzeln und holzigen Knollen im Boden. Dieses Netzwerk von unterirdischen holzigen Sprossachsen und Vorratsorganen bildet den Hauptpool an Biomasse und Kohlenstoffvorräten dieses Ökosystems, der in Kohlenstoffbilanzen von Miombo-Ökosystemen bisher nicht berücksichtigt wird. Um eine Vorstellung von seinem Potenzial für die Kohlenstoffbindung zu bekommen, messe ich im zweiten Aufsatz (Kapitel 3) den unterirdischen Biomassepool und beschreiben die Struktur der unterirdischen Sprossachsen (i.w.S.) von sechs dominanten Arten geoxyler Halbsträucher (je drei von den beiden in unserem Untersuchungsgebiet vorkommenden Bodentypen). Von ferralitischen Böden wurden *Brachystegia russelliae*, *Cryptosepalum exfoliatum* subsp. *suffruticans* und *Syzygium guineense* subsp. *huillensis ausgewählt*, von sandigen Standorten *Parinari capensis*, *Pygmaeothamnus zeyheri* und *Ochna arenaria*. Ich berechne und diskutiere die unterirdische Biomasse und den entsprechenden Kohlenstoffvorrat, dessen Größenordnung mit tropischen Trockenwäldern vergleichbar ist. Sowohl Biomasse als auch das Störungsregime durch Feuer unterscheiden sich zwischen beiden Geoxyle-Vegetationstypen stark.

Ein weiteres wichtiges Merkmal von Geoxyle-Grassländern besteht darin, dass zu jeder Art geoxyler Halbsträucher nahverwandte Baum- oder Straucharten existieren. Der dritte Aufsatz beschreibt und diskutiert die Unterschiede in PFTs von sechs dieser

Vergleichspaare (geoxyle Halbsträucher versus Bäume) im Untersuchungsgebiet Chitembo im Okavango-Einzugsgebiet (Kapitel 4). Wir haben die spezifische Blattfläche (SLA), Blattdicke (LT), Holzdichte (WD), Blattgehalte von Stickstoff (LN), Kohlenstoff (LC), Phosphor (LP), Kalum (LK), Calcium (LCa) und Magnesium (LMg) sowie Blatttrockenmassegehalt (LDMC) gemessen und verglichen. Zusätzlich haben wir das Blattwasserpotential (WP) der Vergleichspaare während der Trocken- und Regenzeit gemessen. Es ist bekannt, dass diese Merkmale Reaktionen auf eine breite Palette von Umweltfaktoren eigen und eng mit ökophysiologischen Mechanismen zusammenhängen. Die Ergebnisse lassen den Schluss zu, dass Unterschiede in funktionellen Merkmalen von geoxylen Halbsträuchern und Bäumen Anpassungen an die spezifischen Umwelteinflüsse ihrer jeweiligen Lebensräume sind.

Im vierten Aufsatz (Kapitel 5) messe und vergleiche ich die funktionellen Eigenschaften (PFTs) von einem erweiterten Set geoxyler Halbsträuchern und nah mit ihnen verwandter Baumarten. Hierfür wurde die Datenbank auf zwölf Arten geoxyler Halbsträucher und vierzehn Baumarten erweitert. Um die unterschiedlichen Anpassungen zu untersuchen, die diese Arten vornehmen können, um mit den Umweltbedingungen ihres Lebensraums umzugehen, wurden Unterschiede der PFTs zwischen Verwandtschaftsgruppen und symbiotischen Strategietypen (Fabaceae versus Nicht-Fabaceae; Ectomycorrhiza assoziierte versus nicht-mykorrhizierte Arten) analysiert und diskutiert. Die Ergebnisse zeigen deutlich ökophysiologische und symbiotische Anpassungen, die sich in bestimmten phylogenetischen Linien während der Evolution entwickelten und es ihnen ermöglichten, die extremen Bedingungen ihrer Lebensräume erfolgreich zu meistern. Die generelle Dominanz von Fabaceen aus der Unterfamilie der Detarioideae auf den nährstoffarmen Böden des Miombogürtels scheint stark durch ihre Ectomycorrhiza-Assoziierung und damit überlegene Phosphoraufnahmefähigkeit bedingt zu sein. Studien aus vergleichbaren Ökosystemen des Miombo-Gürtels wären erforderlich, um diese Hypothese zu erhärten.

Abschließend fasse ich am Ende in einem Synthesekapitel (Kapitel 6) die wichtigsten Ergebnisse meiner vier Aufsätze zusammen und diskutiere sie abschließend.



CHAPTER 1- General introduction

Amândio Gomes

Miombo ecosystems

Miombo ecosystems, dominated by tree species of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia* occupy about 47% of the Angolan territory, mostly on the central Angolan Plateau in the Bié, Huambo and Moxico provinces (Barbosa, 1970). The Angolan miombo woodlands are part of the larger Miombo Ecoregion which covers over 3.8 million km^2 in central and southern Africa, extending from the western escarpment in Angola to the east coast in Mozambique and Tanzania. This ecoregion includes parts of 11 countries: Angola, Namibia, Botswana, South Africa, Zimbabwe, Zambia, Democratic Republic of Congo (DRC), Mozambique, Malawi, Tanzania and Burundi (Timberlake and Chidumayo, 2011).

The Miombo Ecoregion is part of the Southern and Eastern African savannas. Fayolle et al. (2018) divided them into six floristic clusters. In Angola occur mainly three of them, namely the Namibian cluster (*Acacia-Baikiaea* woodlands) in the south-eastern provinces, the South-African cluster (Mopane woodlands) in south-west Angola and the Zambezian cluster (wet Miombo woodlands) in central and eastern Angola. The Zambezian cluster corresponds mostly to White's (1976) "wet miombo" which extends also to northern Zambia, south western Tanzania and central Malawi, in areas receiving more than 1000 mm rainfall per year (Campbel, 1996). This vegetation type is floristically rich and includes most of the characteristic miombo species. Particularly species like *Brachystegia spp.*, *Julbernardia paniculata*, *Isoberlinia angolensis* and *Cryptosepalum exfoliatum ssp. pseudotaxus* are widely distributed.

The central parts of the Angolan Plateau in the Huambo, Bié and Moxico Provinces partly belong to the Okavango catchment which is shared by Angola, Namibia and Botswana. The catchment has large areas which are still in a near-natural state. The Angolan "wet miombo" forms in general a mosaic with open areas of so called "geoxyle grasslands". These are open ecosystems within the miombo woodlands, where geoxyles co-dominate with C4-grasses (Barbosa, 1970). Shaw (1947) described an important type of geoxyle grasslands as "*Anhara de Ongote*", dominated by the geoxyle species *Brachystegia* *russelliae*. These Anhara's de Ongote covers vast treeless valleys with ferralitic soils on the central Angolan plateau. Ongote (or Kassamba) are the local names of *B. russelliae* (in the local cokwe language).

Another important geoxyle dominated vegetation type are the "Chanas da borracha", so-called for frequent occurrence of rubber-yielding Apocynaceae, i.e. of the genera *Landolphia* and *Chamaeclitandra*. This vegetation type prefers sandy soils and is widely distributed in the Lunda and Moxico provinces.

Geoxyles: concepts and terminology

But what are geoxyles exactly? Geoxylic suffrutices (Rietz, 1931; White 1976), in the following termed geoxyles (Lindman, 1914; Simon et al, 2009), have already been discussed in early botanical literature (Schimper, 1898; Warming, 1908). Geoxyles are low-growing woody plants with annual or short-lived shoots sprouting from massive and/or extensive perennial woody underground axes (White 1976). The woody underground organs of geoxyles are diverse, among others xylopodia (Simon et al., 2009), lignotubers (Kolbek and Alves, 2008) and woody rhizomes (Pausas et al., 2018).

A marked characteristic of this life form is the contrast between a reduced development of aerial shoots and the very strong development of woody underground organs (Figure 1), sometimes in the proportions of 1 to 30, measured vertically (Shaw, 1947).

White (1976) pointed out that the stems of geoxyles (in a strict sense) are woody at their base and persist for several years, giving rise to less persistent or herbaceous shoots, which die back after a relatively short time.

The above-ground shoots of geoxyles are very sensitive to fire (White, 1976). Severe fires kill all (sub-)aerial parts, whereupon the plants resprout from belowground bud banks (Pausas *et al.*, 2018). Thus, the geoxyles dealt with in this study frequently burn back to the ground-level in most years and are well adapted to this disturbance regime. Shortly after burning and well before the onset of the rainy season they produce new shoots, which often flower precociously at the base of the shoots. The associated grasses, which when fully grown may conceal the geoxyles to a considerable extent, to begin their vegetative development much later in the season, by which time most suffrutices have already finished flowering (White, 1976) and developed their shoots.

Figure 1: Underground woody rhizome of *Brachystegia russelliae* contrasting with the poorly developed aerial shoots. Photo A. Gomes.

The dominant geoxyle on ferralitic soils besides *Brachystegia russelliae* is *Cryptosepalum exfoliatum* ssp. *suffruticans*. Both species belong to the Detarioid Fabaceae, while Ochnaceae (*Ochna* sp., *Brackenridgea* sp.) and Chrysobalanaceae (*Parinari capensis*) dominate on sandy soils. *Brachystegia russelliae* (ongote), the most dominant geoxyle, grows only some 25 to 35 cm in height. His woody rhizomes grows 5 to 10 cm thick and the patchwork formed in August and September in varying shades of red and green by it's resprouts has been compared to a multi-coloured carpet spread over the ground (Shaw, 1947).

Finally, a distinctive feature of many geoxyles is that they have closely related co-generic tree, shrub or climber species (Figure 2) from which they may have evolved (Burtt-Davy, 1922) or to whom they are at least closely related.


a


b


a1


c


d


e


f

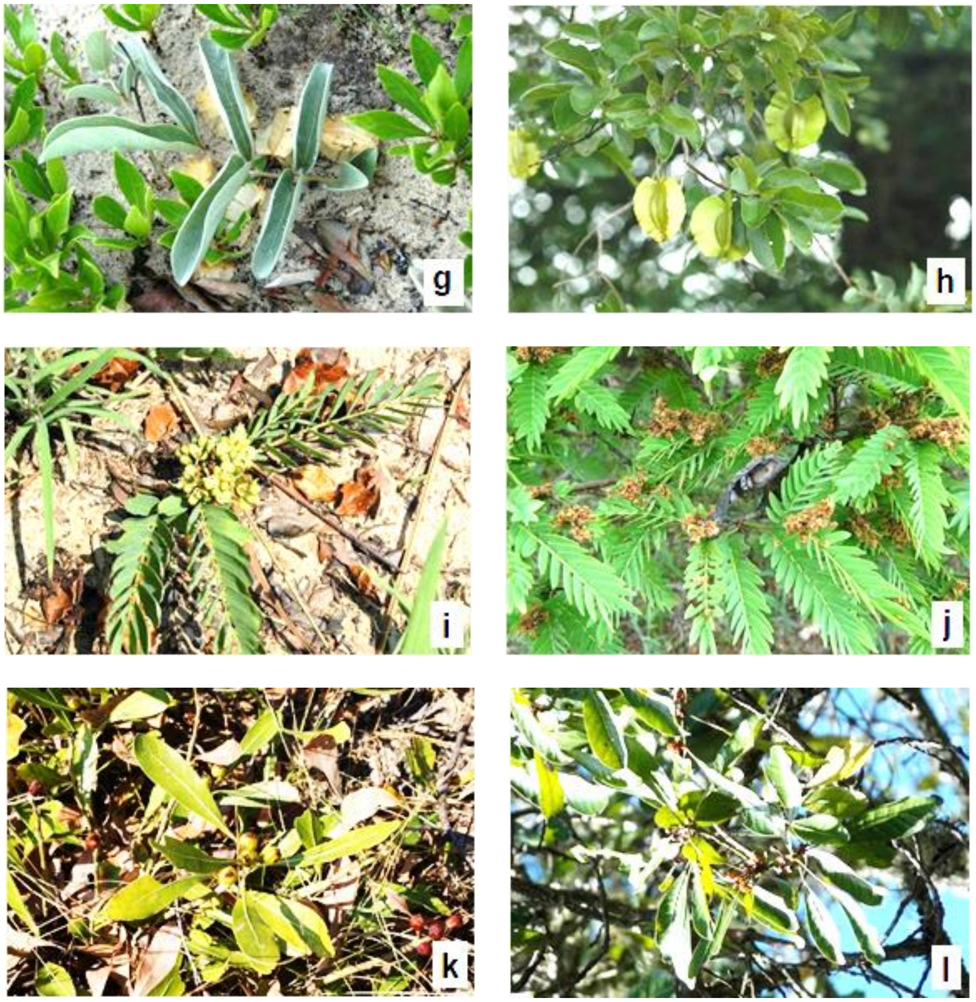


Figure 2: Six pairs of geoxyles and co-generic trees or shrubs which occur together in close distance. a) *Syzygium guineense* subsp. *huillense* with fruits; a1) *Syzygium guineense* subsp. *huillense* in flower; b) *Syzygium guineense* subsp. *guineense*; c) *Cryptosepalum exfoliatum* subsp. *suffruticans*; d) *Cryptosepalum exfoliatum* subsp. *pseudotaxus*; e) *Parinari capensis*; f) *Parinari curatellifolia*; g) *Combretum platypetalum*; h) *Combretum zeyheri*; i) *Brachystegia russelliae*; j) *Brachystegia longifolia*; k) *Uapaca nítida* var. *suffrutescens*; l) *Uapaca nítida* subsp. *nítida*. Photos: A. Gomes and M. Finckh

Diversity and distribution of geoxyles

The global distribution of geoxyles in savanna regions is very uneven (White 1976). Less geoxyle species are described from South America than from tropical south-central Africa. In many cases the South American species are taxonomically isolated, obligate suffrutices and less well represented than the species in tropical Africa. However, geoxyles are a conspicuous feature of the Brazilian Cerrado. Only few geoxyles are found in tropical Asia and they seem to lack completely in Australia (Clarke et al. 2015). A few geoxyles occur in arctic-alpine environments, among others in the genera *Salix* and *Betula*.

White (1976) discussed the diversity, origin and adaptive advantages of the geoxyle flora of tropical south-central Africa where its greatest diversity is found. He listed no less than 109 species belonging to 56 genera from 31 families, finding them mostly confined to the two savanna phytoregions: the Sudanian and the Zambezian phytoregion (White, 1976). The Sudanian phytoregion is a wide belt north of the equator between the rainforests of the Guineo-Congolian Region and the arid regions to the north, most of it lowlands. The Zambezian phytoregion on the other hand occupies a comparable position south of the equator, most of it highlands. The Zambezian phytoregion is considered to be 15 times as geoxyle rich than the Sudanian phytoregion which comprises mainly lowlands. Until today, White's (1976) list has been expanded to 198 species (Maurin et al., 2014, Zigelski et al., 2019, own data).

White (1976) stated that the great majority of geoxyles occurring in the Zambezian region were to be found within the range of the former distribution of Kalahari sands. However, geoxyles occur in Angola in grasslands all over the highlands of Huíla, the Bié plateau, the Malange plateau, the Lunda provinces and in the upper Zambezi and Luena Basin in north-eastern Moxico at altitudes between 900 and ca. 2250 m. Geoxyles are especially abundant near the ridge lines that separate the basins of the rivers Kwanza, Keve, Catumbela, Cunene and Kubango, usually appearing in red soils of the ferralitic group or in contact with Kalahari sands (Barbosa, 1970).

Ecology of geoxyles

According to White (1976), the most characteristic habitat of geoxyles in the Zambezian region are seasonally anaerobic grasslands, mostly on sandy, extremely oligotrophic soils, which are waterlogged and badly aerated for parts of the year. Such habitats were to find at the ecotone of Zambezian woodlands and the edaphic grassland of waterlogged depressions (Dambos). However, these conditions do not apply to the typical geoxyle grasslands on the slopes of the Angolan plateau, were soils of most geoxyle grasslands are well drained and do not show hydromorphic patterns.

Geoxyles are normally absent from secondary grasslands which develop after the destruction of forests and woodlands and they are only found on nutrient poor and unfertilized soils (White, 1976).

The evolutionary drivers of the geoxylic life form have intrigued researchers for a long time. Most researchers hypothesised geoxyles to be plants' response to adverse environmental factors like fire, frost, herbivory, edaphic conditions and/or others (Burtt-Davy, 1922; White, 1976; Barbosa, 1970). Barbosa (1970) suggested that the geoxylic habit is probably the result of strong fluctuations of the soil water level and temperature (flooding in the hot summer and drought during the cold winter) associated with hydromorphic shallow soils. Maurin et al. (2014) dismissed herbivory and frost as evolutionary drivers of the geoxylic life form, suggesting instead an interaction of fire frequency and high precipitation as main drivers. Finckh et al. (2016) disagreed and pointed at frost as the main evolutionary driver, based on studies from the Angolan highlands. These conflicting hypotheses indicate the need of further research to better understand ecology and evolutionary background of this fascinating life form.

This lack of knowledge and understanding on basic functional aspects of geoxyle ecology is one of the main motivations for my thesis. The chapters 4 and 5 will address this research gap.

Ecosystem functions and services of geoxyle grasslands

In recent decades the multiple benefits provided by ecosystems and landscapes gained the attention of scientific and stakeholder audiences. The resulting discussions on ecosystem functions and services (ESF/ESS) provided the basis for the Millennium Ecosystem Assessment (2005). This first global assessment classified ecosystem services into four categories: (1) **provisioning services**, the direct supply of goods to people, often with a notable monetary value, such as timber from forests, medicinal plants from all types of natural vegetation, and fish from oceans, rivers and lakes; (2) **regulating services**, the range of functions carried out by ecosystems which maintain the biosphere but are generally not given a monetary value in conventional markets. They include climate regulation through carbon storage and control of local rainfall, the removal of pollutants by filtering air and water, and protection from disasters via stabilisation of slopes and coastlines; (3) **cultural services**, not providing direct material benefits, but contributing to wider needs and desires of the society, and therefore to people's willingness to pay for conservation. They include the spiritual value attached to particular ecosystems such as sacred groves, and the aesthetic beauty of landscapes or coastal formations that attract tourists; (4) **supporting services**, not of direct benefit to people but essential for the functioning of ecosystems and therefore indirectly responsible for all other services. Examples are the formation of soils and the processes of plant growth.

Miombo ecosystems, including geoxyle grasslands, supply many products and services which are essential for the well-being of rural and urban communities. Miombo woodlands constitute the main source of woodfuel and provide a wide range of non-timber products (Brigham et al., 1996). The population resident in the miombo region obtains the majority of their livelihood needs directly or indirectly from the goods and services provided in miombo ecosystems (Gauslaa 1989; Dewees 1994; Morris 1995). This includes provisioning services via cropping, grazing, collection and sale of a variety of woodland and grassland resources, as well as regulating services such as water provision, nutrient cycling, and carbon sequestration (Williams et al., 2008; Shirima et al., 2011; Ribeiro et al., 2015; Ryan et al., 2016). In studies carried out in Angola (Firmino, 2016; Baptista, 2014; Domptail et al, 2013) and Namibia (Pröpper et al., 2013), ecosystem services and functions provided by miombo ecosystems were regarded as important source of subsistence, supporting the livelihoods of people in the Okavango region.

Meanwhile, most studies related to miombo products and services neglected the ESF/ESS provided by geoxyle grasslands in the region. However, geoxyles provide products and services essential for local populations. Several species have edible fruits, which are a valuable source of nutrition for rural communities (Figure 3). Important examples of fruit-bearing geoxyles are *Diospyros chamaethamnus*, *Pygmaeothamnus zeyheri*, *Annona stenophylla, Lannea edulis, Landolphia gossweileri, Chamaeclitandra henriquesiana, Parinari capensis, Syzygium guineense* subsp. *huillense* and many more (Figure 3). There are also geoxyles and other plant species from geoxyle grasslands which are used as medicine by rural communities and sold in urban markets (Domptail et al., 2013).

Geoxyle grasslands also provide relevant regulating services, e.g. by carbon storage. The extended network of belowground roots, rhizomes and lignotubers constitutes an important stock of carbon whose contribution to global carbon accounts has been ignored so far (but see chapter 3). Besides, geoxyles stabilise the topsoil and thus protect soils from erosion through heavy tropical downpours. According to our observations, once broken by modern agricultural machinery, erosion lines appear and progress quickly, developing over time in ravines and gullies, a very frequent phenomenon in the sloping areas with ferralitic soils on the Bié plateau.

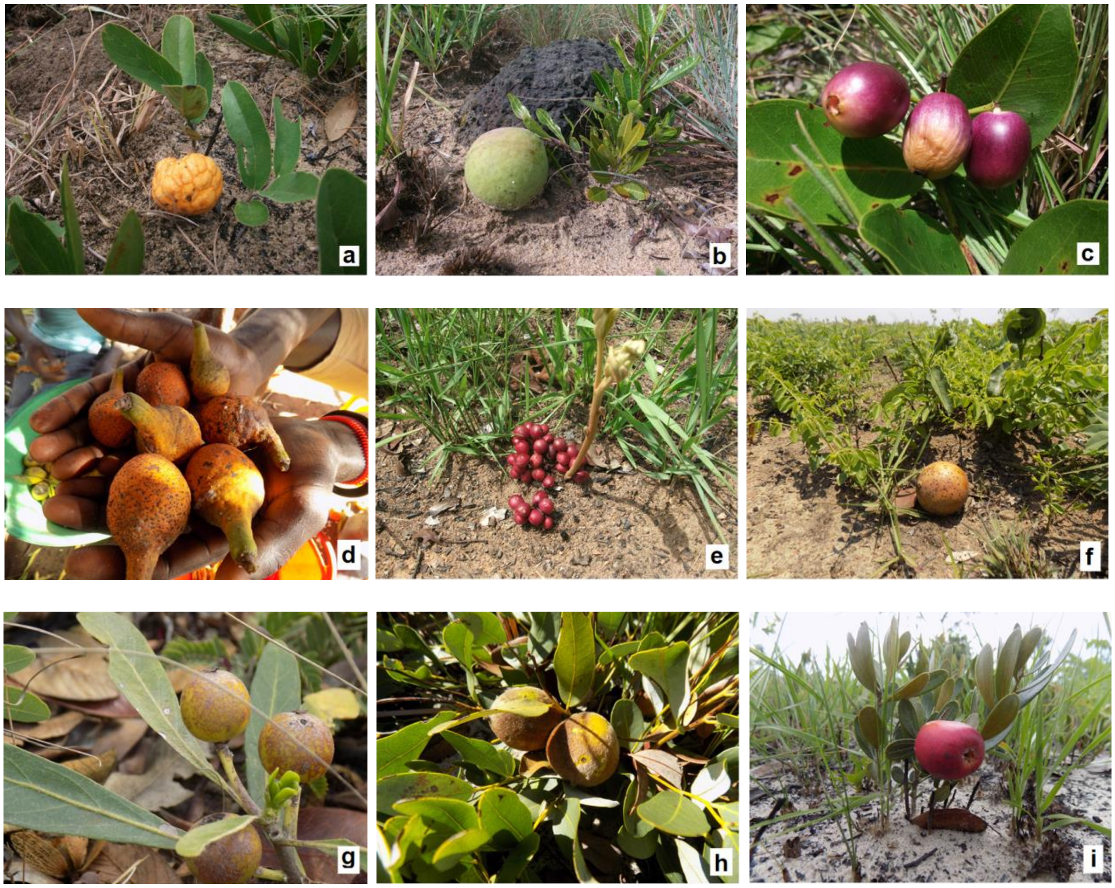


Figure 3: Edible fruits of geoxyles from Cusseque. a- *Annona stenophylla*; b- *Landolphia gossweileri*; c- *Syzygium guineense* subsp. *huillense*; d- *Chamaeclitandra henriquesiana*; e- *Lannea edulis*; f- *Strychnos* sp.; g- *Uapaca nitida* var. *suffrutescens*; h- *Diospyros chamaethamnus*; i- *Anisophyllea quangensis*. Photos A. Gomes

Aims and structure of the thesis

The overall aims of my thesis are (1) to give an update on diversity and distribution of geoxyle co-dominated ecosystems in Angola; (2) to look at vegetation dynamics, root structure, belowground biomass and soil characteristics of the geoxyle dominated ecosystems; (3) to look at the role of functional traits in a pairwise comparison between closely related geoxyles and trees; and finally (4) to look at life form- and lineage-specific plant functional trait adaptations of a large set of frequent geoxyles and trees in my study area at Cusseque (Chitembo, Bié).

These aims are addressed in the following sequence:

Chapter 1 gives a general introduction into the conceptual framework used for the present study with a special focus on the miombo ecoregion, the geoxyle life form and geoxyles´ diversity, distribution and ecology.

Chapter 2, Geoxyle dominated ecosystems in Angola. This chapter provides an overview of the Angolan geoxyle dominated ecosystems and its diversity. Species composition, endemism, and environmental conditions are the focus of this introductory chapter.

Chapter 3, Vegetation dynamics, root structure, belowground biomass and soil characteristics of geoxyle grasslands on the Bié Plateau. In this chapter I address the vegetation (and disturbance dynamics) of geoxyle ecosystems, the characterisation and quantification of their biomass pools, and some key soil properties of these ecosystems. A large proportion of the geoxyle biomass is hidden in the upper soil horizons, forming a complex network of woody roots, shoots and lignotubers.

Chapter 4, Tree or not tree: differences in functional traits among geoxyles and closely related trees species. As described above, many geoxyles of the Angolan plateau occur together with closely related tree species in adjacent woodlands. To better understand the functional advantages of the geoxyle life form, this chapter addresses pairwise comparisons of 12 plant functional traits among 6 pairs of geoxyles and trees, in order to analyse the functional differences (and respective habitat specific advantages) of the two life forms.

Chapter 5, Functional traits and symbiotic associations of geoxyles and trees explain the dominance of detarioid legumes in miombo ecosystems. In this chapter I finally analyse plant traits to evaluate the role of symbiotic associations for the hyperdominance of detarioid legumes in both, miombo woodlands and adjacent geoxyle grasslands.

Chapter 6) Synthesis. This concluding chapter gathers the current knowledge on diversity, ecology, and evolutionary history of geoxyles and geoxyle dominated ecosystems in Angola and points at important knowledge gaps.

Project context and study area

This thesis has been conducted as part of the transdisciplinary The Future Okavango (TFO) project (Figure 4), funded by the German Federal Ministry of Education and Research (BMBF) under the umbrella initiative Research for Sustainable Development (FoNa). To implement the TFO project, four core research sites were initially selected representing diverse social-ecological systems from the entire Okavango basin. Two of these research sites were located in Angola, Chitembo (in the headwater region of the Okavango) and Caiundo (at the middle section of the river). Field work has been carried out in a collaborative context of international and Angolan scientists with support by field assistants from the local communities.

Field work for this thesis was mostly conducted at the Cusseque core research site, an area of 100 km² located in the Chitembo Municipality, Bié Province. Specifically, the research site was located at the Cusseque River along the main road EN140 between Chitembo and Mumbué (Figure 4).

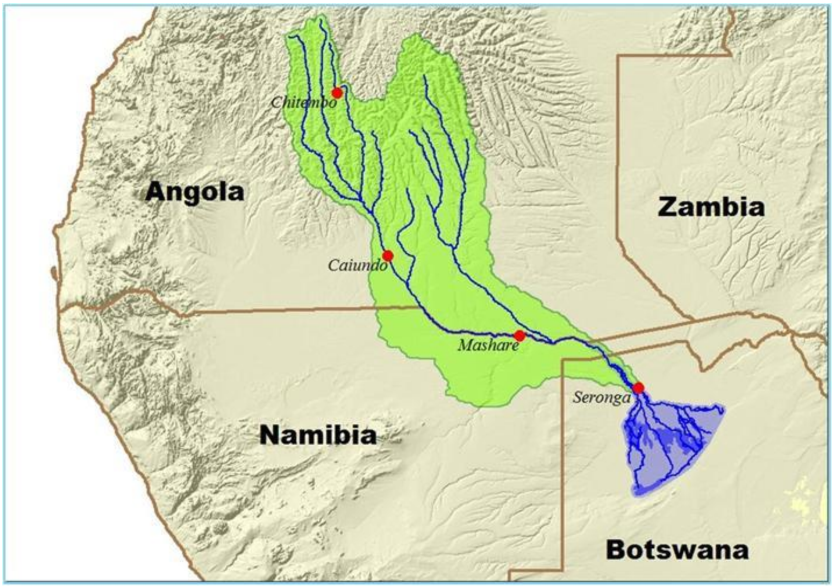


Figure 4: Map of the Future Okavango Research Area (FORA) in southern Africa (green) including the Okavango delta in Botswana (blue), Source: <http://www.future-okavango.org>.

The landscape of the study area can be described as rolling hills on the southern slopes of the Bié-Plateau, intersected by the north to south stretching Cusseque River and its perpendicular tributaries. The mean elevation is 1,575 m above sea level, with a difference in elevation between the Cusseque valley and the surrounding hills of about 100 m (Gröengröeft et al. 2013 b).

The climate on the Angolan Central Plateau is semi-humid with a pronounced wet season lasting from November to April. The mean annual temperature of the Cusseque area is ca. 20.4°C with an annual precipitation of about 990 mm (Weber 2013). Night frost is frequent during the dry season, particularly in June and July (Revermann & Finckh, 2013).

The Cusseque site presents a high pedodiversity. The elevated areas on the hills are characterized by slightly loamy Arenosols, overlying weathered granitic bedrocks. The slopes of the smaller tributary valleys show shallow Plinthisols on granitic bedrocks. The soils along the eastern part of the Cusseque River are characterized by very deep and leached Arenosols. Along the rivers and smaller streams we find linear 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. 2013 a).

The main vegetation types of the study area are semi-deciduous miombo woodlands and forests, interspersed with geoxyle grasslands in the valleys.

Further information on the natural history of the Cusseque site is given in chapters 3, 4 and 5.

Four small villages are found within the research site Cusseque: Sovi, Cahololo, Cusseque and Calomba. The human population mostly belongs to the ethnic Chokwe group. Subsistence agriculture based on shifting cultivation is their main source of livelihood, with maize (*Zea mays*), cassava (*Manihot esculenta*), beans (*Phaseolus vulgaris*) and peanut (*Arachis hypogaea*) being the main crops. Other sources of income include small livestock, wage labour and, notably in the nearby town of Chitembo, the retail of natural resources like charcoal, bushmeat and honey (Domptail et al., 2013).

CHAPTER 2- Geoxyle co-dominated ecosystems

Paulina Zigelski, Amândio Gomes and Manfred Finckh

Biodiversity of Angola, Science and Conservation: A Modern Synthesis

Abstract A small-scale mosaic of miombo woodlands and open grasslands is a typical aspect of the Zambezian phytochorion that extends into the eastern and central parts of Angola. The grasslands are home to so-called ‘underground trees’ or geoxyles, a life form with massive underground wooden structures. Some (but not all) of the geoxyles occur also in open woodland types. These iconic dwarf shrubs evolved in many plant families under similar environmental pressures, converting the Zambezian phytochorion into a unique evolutionary laboratory. In this chapter we assemble the current knowledge on distribution, diversity, ecology and evolutionary history of geoxyles and grasslands in Angola and highlight their conservation values and challenges.

Keywords Endemism; Geoxyles; Miombo; Phytochorion; Underground forests; Vegetation.

Open grassy vegetation is a common aspect of Angolan landscapes and is a characteristic part of the Zambezian phytochorion. Grasses are the most conspicuous element of these landscapes towards the end of the rainy season, whereas at the onset of the rainy season many woody species of so called geoxyles or ‘underground trees’ (Burt-Davy 1922; White 1976) dominate the aspect of the vegetation. Thus, in vast areas of central and eastern Angola, the open ‘grasslands’ are de-facto co-dominated by grasses and geoxyles. Closely intertwined with miombo woodlands and with wetlands, geoxyle grasslands constitute one of the main and most particular ecosystem types of Angola. According to Mayaux et al. (2004), they cover at least 70,080 km2 or 5.6% of the Angolan territory (not including the small scale woodland geoxyle grassland mosaics of the central Angolan plateau).

The geoxyle life form is marked by proportionally massive underground woody organs, in literature often termed as lignotuber*,* xylopodia or woody rhizomes. Annual shoots sprout readily from the buds on these perennial woody organs, bearing leaves, inflrescences and fruits before they die back after the end of the rainy season. Coexistence of grasses and suffrutices is made possible by occupation of different ecological niches together with phase-delayed activity periods (i.e. main assimilation/flwering/fruiting time) that reduces competition.

Exploration of geoxyle grasslands

The first authors who indicated the distribution and ecological particularity of geoxyle grasslands in Angola were Gossweiler and Mendonça (1939), who classifid them as heathland-like woodlands (‘Ericilignosa’). They already noted the main differentiation between the *Cryptosepalum* and *Brachystegia* dominated geoxyle communities (‘Anharas de Ongote’) on ferralitic and psammoferralitic soils and the vegetation types characterised by *Parinari capensis* and the Apocynaceae *Landolphia thollonii* and *L. camptoloba* on leached sandy soils (‘Chanas da Borracha’). They had also already observed the strong thermic oscillations of which at least the ‘Anharas de Ongote’ are subject (see below) and commented on the generative cycle of *Brachystegia russelliae* from flowering to fruiting in the dry season (and thus, being inverse to the generative cycle of the C4-grasses).

Using a different mapping and classifiation approach, typical geoxyle grassland mostly on sandy soils were again mapped and described by Barbosa (1970) as ‘Chanas da Borracha’ (alluding to the presences of species of the genus *Landolphia*), ‘Chanas da Cameia’, and ‘Anharas do Alto’. The *Cryptosepalum* spp. dominated ‘Anharas de Ongote’ on ferralitic soils are described (but not depicted on the map) as being inserted in the main miombo types of the Angolan plateau. However, he describes the typical spatial pattern, i.e. how they appear closes to the headwaters of the small tributaries and then follow the watercourses in narrow or broad fringes downstream. Gossweiler and Mendonça (1939) as well as Barbosa (1970), treated these ecosystems as particular site specific plant communities closely linked to woodland ecosystems, and not as grass-dominated savannas.

White (1983), however, mapped and described only the sandy ‘Chanas’ as ‘Kalahari and dambo-edge geoxylic grassland’ in the context of the ‘Zambezian edaphic grassland’, but did not refer to the ‘Anharas de Ongote’ which constitute a key (but small scale) element of the miombo ecosystems of the Angolan plateau. Even in his prominent suffrutex review, White (1976) focuses solely on the ‘Chanas’ in the range of the Zambezi Graben and neither mentions (psammo-) ferralitic ‘Anharas’, nor lists their dominant key species *Brachystegia russelliae* and *C. exfoliatum* ssp. *suffruticans* in his geoxyle list. He certainly recognises a transition zone between Zambezian and Guineo-Congolian floras that spans over central and northern Angola (where the ‘Anharas’ are included) (White 1983). However, he did not recognise the importance and floristic singularity of the ferralitic geoxyle grasslands dominated by *Cryptosepalum* spp.

Geoxyle flora and endemism

The geoxyle life form appears in many different floristic groups and obviously evolved convergently. A similar center of geoxyle diversity has been reported from the Brazilian Cerrado. Today, 198 species from 40 families are listed for the western Zambezian phytochorion (White 1976; Maurin et al. 2014, own data), but an even higher number is expected as floristic exploration of the region is still poor and new species might be found (see Goyder and Gonçalves 2019). In some cases geoxyles are considered a dwarf variety or subspecies of a closely related tree species (e.g. *Gymnosporia senegalensis* var. *stuhlmanniana*, *Syzygium guineense* ssp. *huillense*) and hence classifid as such and not as one species, although the genetic relatedness between tree and dwarf form is rarely investigated. On the other hand, not all dwarf forms are obligate suffrutices; some can facultatively outgrow the dwarf state if protected from environmental stressors (White 1976), for instance *Oldfildia dactylophylla* or *Syzygium guineense* ssp. *macrocarpum* (Zigelski et al. 2018).

Within the geoxyle communities of the Zambezian phytochorion, the Rubiaceae have the highest number of described taxa (46), followed by Anacardiaceae (22) and Lamiaceae (14). Table 1 lists all families with known geoxyle taxa occurring in Angola and gives examples of common geoxyles for each family. Furthermore, Figure 5 shows some examples and aspects of geoxyle species given in Table 1. The unique Zambezian geoxylic flora with a high number of endemic species (Brenan 1978; White 1983; Frost 1996) is a consequence of challenging environmental conditions, as illustrated further below. According to Figueiredo and Smith's catalogue of Angolan plants (2008) and our list of suffrutices (Table1), 121 of the 198 geoxyle species occurring in the Zambezian phytochorion are known from Angola (61%). Of these 121 species 12 are endemic to Angola (10%).

Environmental conditions of geoxyle grasslands through the year

The substrate strongly inflences the species composition of the geoxylic grassland. In Angola geoxyles occur on (a) well-drained arenosols which are found as seasonally floded savannas in the Zambezi Graben of the Moxíco province or as sandy alluvial deposits on fossil river terraces along the valleys of the southern slopes of the Angolan plateau (Figure 6 a); (b) on psammo- ferralitic plinthisols as they frequently occur on the Bíe Plateau in central Angola. The geoxyle grasslands on ferralitic soils mostly occur on mid- and foot-slopes and are embedded within a matrix of miombo woodland (Figure 6 b).

Environmental conditions in geoxyle grasslands change dramatically throughout the year. The most perceived stresses are man-made fires in the dry season (May–October) which are mostly deployed to induce resprouting for livestock fodder or to facilitate hunting (Hall 1984). Depending on fire intensity, which in turn depends mostly on fuel load, ambient temperature and wind (Govender et al. 2006), such fires can completely burn unprotected aboveground biomass.

Table 1: List of plant families with geoxyles in the Zambezian phytochorion.

Plant family	n	Species commom in Angola	Angolan endemics
Rubiaceae	46	*Pygmaeothamnus zeyheri* (Sond.) Robyns, *Pachystigma pygmaeum* (Schltr.) Robyns	2, e.g. *Leptactina prostrata*
Anacardiaceae	22	*Lannea edulis* (Sond.) Engl., *Rhus arenaria* Engl.	3, e.g. *Lannea gossweileri*
Lamiaceae	14	*Clerodendrum ternatum* Schinz, *Vitex madiensis* ssp. *milanjensis* (Britten) F.White	
Fabaceae-Papilionioideae	13	*Erythrina baumii* Harms, *Abrus melanospermum* ssp. *suffruticosus* Hassk.	3, e.g. *Adenodolichos mendesii*
Proteaceae	11	*Protea micans* ssp. *trichophylla* (Engl. & Gilg) Chisumpa & Brummitt	1, *Protea paludosa* (Hiern) Engl.
Ochnaceae	9	*Ochna arenaria* De Wild. & T. Durand, *Ochna manikensis* De Wild.	
Passifloraceae	7	*Paropsia brazzaeana* Baill.	
Fabaceae-Detarioideae	6	*Brachystegia russelliae* I.M. Johnst., *Cryptosepalum exfoliatum* ssp. *suffruticans* (P.A.Duvign.)	
Apocynaceae	5	*Chamaeclitandra henriquesiana* (Hallier f.) Pichon	1, *Landolphia gossweileri*
Ebenaceae	5	*Diospyros chamaethamnus* Mildbr, *Euclea crispa* (Thunb.) Gürke	
Celastraceae	4	*Gymnosporia senegalensis* var. *stuhlmanniana* Loes.	
Dichapetalaceae	4	*Dichapetalum cymosum* (Hook.) Engl.	
Fabaceae-Caesalpinioideae	5	*Entada arenaria* Schinz, *Bauhinia mendoncae* Torre & Hillc.	
Myrtaceae	4	*Syzygium guineense* ssp. *huillense,* (Hiern) F. White, *Eugenia malangensis* (O.Hoffm.) Nied.	
Tiliaceae	4	*Grewia herbaceae* Hiern	
Combretaceae	3	*Combretum platypetalum* Welw. ex M. A. Lawson	2, e.g. *Combretum argyrotrichum*
Euphorbiaceae	3	*Sclerocroton oblongifolius* (Müll.Arg.) Kruijt & Roebers	
Loganiaceae	3	*Strychnos gossweileri* Exell	

Annonaceae	2	*Annona stenophylla* ssp. *nana* (Exell) N. Robson	
Apiaceae	2	*Steganotaenia hockii* (C. Norman) C. Norman	
Chrysobalanaceae	2	*Parinari capensis* Harv., *Magnistipula sapinii* De Wild.	
Meliaceae	2	*Trichilia quadrivalvis* C.DC.	
Moraceae	2	*Ficus pygmaea* Welw. ex Hiern	
Myricaceae	2	*Morella serrata* (Lam.) Killick	
Phyllanthaceae	2	*Phyllanthus welwitschianus* Müll.Arg.	
Ranunculaceae	2	*Clematis villosa* DC.	
Achariaceae	1	*Caloncoba suffruticosa* (Milne-Redh.) Exell & Sleumer	
Anisophyllaceae	1	*Anisophyllea quangensis* Engl. ex Henriq.	
Clusiaceae	1	*Garcinia buchneri* Engl.	
Dilleniaceae	1	*Tetracera masuiana* De Wild. & T. Durand	
Hypericaceae	1	*Psorosperum mechowii* Engl.	
Ixonanthaceae	1	*Phyllocosmus lemaireanus* (De Wild. & T. Durand) T. Durand & H. Durand	
Lecythidaceae	1	*Napoleonaea gossweileri* Baker f.	
Linaceae	1	*Hugonia gossweileri* Baker f. & Exell	
Malpighiaceae	1	*Sphedamnocarpus angolensis* (A. Juss.) Planch. ex Oliv.	
Malvaceae	1	*Hibiscus rhodanthus* Gürke	
Melastomaceae	1	*Heterotis canescens* (E. Mey. ex Graham) Jacq.-Fél.	
Picrodendraceae	1	*Oldfildia dactylophylla* (Welw. ex Oliv.) J.Léonard	
Rhamnaceae	1	*Ziziphus zeyheriana* Sond.	
Urticaceae	1	*Pouzolzia parasitica* (Forssk.) Schweinf.	

Note: Nº: Overal number of geoxyle species in the Zambezian phytochorion; examples of species occuring in Angola are given for each family. Compilation of families and species according to White (1976), Maurin et al. (2014) and own data.

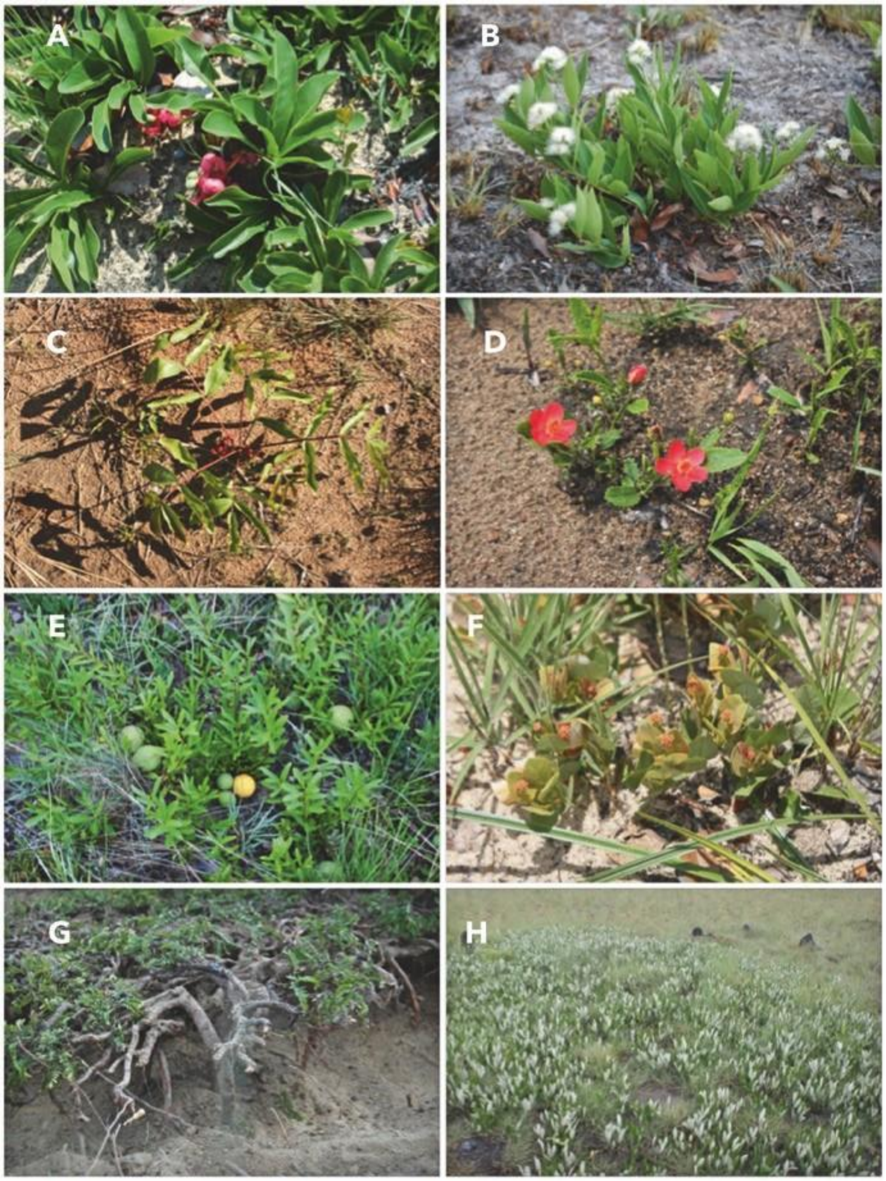


Figure 5. Common Angolan geoxyle species. (a) *Ochna arenaria* (Ochnaceae), fruiting and growing on sandy sediments of the Bíe Plateau. (b) *Syzygium guineense* ssp. *huillense* (Myrtaceae) flwering in the dry season and growing on sandy soils of the Bíe Plateau. (c) *Lannea edulis* (Anacardiaceae), bearing edible fruits, growing on Kalahari sands in southeast Angola. (d) *Hibiscus rodanthus* (Malvaceae), growing on Kalahari sands in southeast Angola and flwering in the rainy season. (e) *Landolphia gossweileri* (Apocynaceae), typical element of the 'Chanas da Borracha', growing on sandy soils of the Bíe Plateau and bearing edible fruits. (f) *Phyllanthus welwitschianus* (Phyllanthaceae), growing on sandy soils of the Bíe Plateau and flwering in the

rainy season. (g) *Cryptosepalum exfoliatum* ssp. *suffruticans* (Fabaceae – Detarioideae) with excavated rootstocks, typical element of the 'Anharas de Ongote', growing on psammoferralitic soils of the Bíe Plateau. (h) *Parinari capensis* (Chrysobalanaceae), typical element of the 'Chanas da Borracha', growing on slightly elevated termite mounds in floded savannas of the Cameia National Park, Moxico Province.

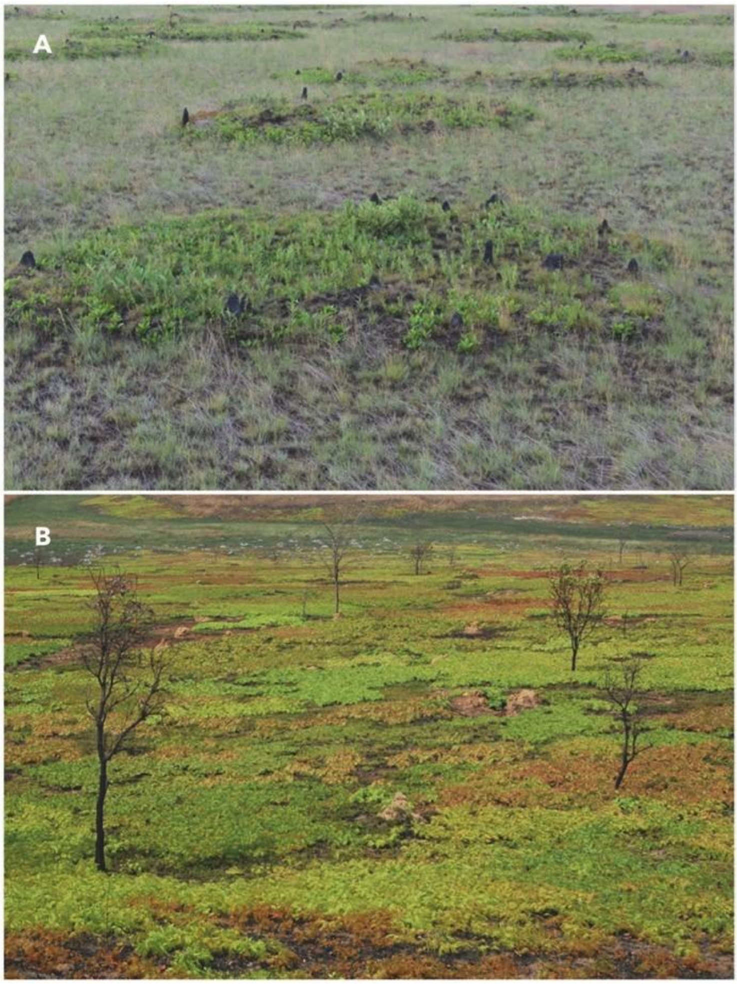


Figure 6. Typical geoxyle grassland of Angola. (a) 'Chanas da Cameia' in the Cameia National Park, Moxíco Province, during dry season in June. The slightly elevated termite mounds provide habitat for several geoxyle species that avoid the low-lying areas that are waterlogged from January to May. (b) 'Anharas de Ongote' in the Sovi Valley on the southern slopes of the Bíe Plateau, in August. The mid- and footslopes are dominated by suffrutex-grassland with the characteristic reddish and green patches of the fresh leaves of *Brachystegia russelliae*, whereas the wetlands in the drainage lines are covered mostly by Cyperaceae (background, in dark green).

Another abiotic stress occurring mostly in the early dry season (June–August) is nocturnal frost, peaking immediately before sunrise. At this time of year masses of cold dry air from southern latitudes intrude into south-central Africa (Tyson and Preston-Whyte 2000). As depressions accumulate confluent cold air, the undulating topography of the Angolan highlands facilitates frequent radiation frost especially in valleys (Revermann and Finckh 2013; Finckh et al. 2016). Up to 44 frost events per dry season (with a minimum temperature of −7.5 °C) were recorded by Finckh et al. (2016), with a temperature span of up to 40 degrees within 12 h. Most woody species from tropical background (including geoxyles) are sensitive to frost, their leaves wilt or their shoots die-off entirely.

The geoxyle species seem to be triggered by the destruction of their shoots by frost and/or fire, as they readily resprout after these disturbances and in most cases already start flwering in the dry season. The geoxyles therefore have often already finished their generative cycle when the grasses start to cover them.

The geoxyles of the sandy plains in eastern Angola are furthermore subject to seasonal floding in the late rainy and early dry season (January–May), leading, for example, in the Cameia National Park to standing water up to 0.5 m deep. Whereas grass species dominate the sites which are inundated for several months, geoxyle species seem to avoid fully waterlogged sites and grow patchily on slightly elevated termite mounds (Figure 6 b) or other well drained sites.

The dominant grass species seem to profit from inundation. Their tufts develop massively in the middle of the rainy season and they flower and bear fruits throughout the flooding season (own observations).

Knowledge gaps on the evolution of the geoxyles and the formation of geoxyle grasslands

A common observation within geoxyle ecosystems is the resemblance (Meerts 2017) and assumed close relatedness of geoxyle species to tree species that occur in forests and woodlands. The indigenous people (e.g. the Chokwe in eastern Angola) in many cases recognise the similarity and relatedness and use similar local names for such pairs, for instance *Muhaua* and *Mupaua* for the tree and geoxyle forms of *Syzygium guineense* Willd. DC. The striking fact that the suffrutex life form was developed by several plant families independently and at roughly the same time (Maurin et al. 2014) indicates a common driver that triggered its convergent evolution.

Grassy biomes emerged in Africa in the late Miocene approximately 10 mya (Cerling et al*.* 1997; Keeley and Rundel 2005; Herbert et al. 2016). This period is characterised by global climatic fluctuations which led to cooler, drier conditions, to a drop of atmospheric CO_2 concentrations and particularly to pronounced precipitation seasonality (i.e. wet and dry seasons) in southern Africa (Pagani et al. 1999). As a consequence, humid tropical forests retreated to more favorable sites further north and were replaced by more open dry and seasonal tropical forest ecosystems like the miombo (Bonnefile 2011). In parts where miombo landscapes prevail today, canopies were disrupted and allowed the establishment of open ecosystems embedded in woodland matrices. These open ecosystems were then rapidly occupied by lightdemanding C4-grasses and the evolving geoxyles.

It is still an open discussion why open geoxyle grasslands are able to persist within the woodlands (or vice versa). It is however likely that rainfall seasonality and the above described abiotic stresses that characterise the geoxyle grasslands play a major role in their establishment and maintenance (Sankaran et al. 2005; Staver et al. 2011).

Savanna ecologists tend to see fire as the main driver for grassland formation. On the one hand frequent fires prevent tree establishment if saplings cannot outgrow the reach of the flmes and are destroyed therein. For woodlands in eastern South Africa, a fire free time period of at least 5 years is necessary for many tree species to escape the ‘fire trap’ (Sankaran et al*.* 2004; Gignoux et al*.* 2009). This time window, allowing for successful reestablishment of trees, is rarely achieved in Angolan grasslands, at least nowadays (Schneibel et al*.* 2013; Stellmes et al. 2013). C4-savanna grasses, however, respond positively to periodic burning and resprout within weeks (Bond and Keeley 2005), thus being able to colonise seasonally burnt sites.

Forest ecologists, on the other hand, attribute the frequent short duration frost events in the dry season for preventing tree recruitment in the open areas (Finckh et al. 2016). As the list of geoxyles (Table 1) shows, mainly (but not exclusively) tropical families or genera evolved suffrutex life forms. Frost is deleterious to most tropical tree taxa, as they have not developed physiological adaptations to this ‘untropical’ stress factor, thus showing little or no frost tolerance (Sakai and Larcher 2012). As the geoxyle grasslands are typically situated in particularly frost prone sites (depressions), tree taxa that are not adapted to frost are being filtered out of such environments.

In any case, a promising strategy to cope with seasonally returning thermic stress (by frost or fire) is to protect sensitive organs (buds) by hiding them underground. Tree species relocated their woody biomass and regenerative buds belowground at the expense of growth height and were thus able to cope with frost and fire prone sites (White 1976; Maurin et al. 2014; Finckh et al. 2016). Even shallow soil depths of less than 10 cm are sufficient to alleviate thermic stresses (Revermann and Finckh 2013). The high number of tropical genera and families that contribute to the geoxyle flora show how successful this strategy is for frost sensitive and fire susceptible taxa, in order to survive the adverse conditions of the open grasslands.

Concomitantly other evolutionary advantages of the geoxylic life form have been discussed, for instance poor edaphic conditions, as favoured by White (1976). He considered the low nutrient status of the leached and locally seasonal waterlogged soils on Kalahari sands as a likely cause for the lack of regular trees and the suffrutication of them as means of compensation. However, trees as well as geoxyles often grow on the same or similarly poor soils, with comparable physical and chemical properties (Gröngröft et al. 2013); forests and grasslands are not separated by edaphic boundaries but follow topographic rather than edaphic logics.

The waterlogging argument on the other hand would imply that the woody underground organs show adaptations to inundation, for instance aerenchymatic tissue or adventitious roots (Parolin 2008). Anatomical analyses of the rootstocks of four common geoxyles species however did not provide any support for aerenchymatic tissue nor other adaptations to inundation (Sanguino 2015). Moreover, in seasonally floded savannas geoxyles avoid inundated sites. This is even the case for *Syzygium guineense* ssp. *huillense*, a geoxyle closely related to a tree species that grows along and in rivers and floodplains (Coates Palgrave 2002; Meerts and Hasson 2016).

To summarise, so far the main environmental driver for the astonishing radiation of geoxyles has not been conclusively identifid. The emergence of the geoxyle grassland at the end of the Pliocene and the peak of radiation at the beginning of the Pleistocene is clearly related to climatic seasonality and pronounced dry seasons. Dry seasons, however, did not only provide the necessary dry fuel for fire but also provided the atmospheric conditions for nocturnal frost events – the seasonality argument, thus, do not tip the balance toward fire or frost.

Conservation value and conservation challenges

Various studies recognise the high floristic singularity of the Zambezian phytochorion and geoxyle grasslands with its unique life forms contribute prominently to its high number of endemic species (Clayton and Cope 1980; White 1983). The high degree of geoxyle endemics within the Zambezian phytochorion as well as within Angola is a consequence of a unique setting of environmental drivers like nutrient poor soils, frequent frosts and fires or precipitation seasonality in a small-scale heterogeneous landscape (Linder 2001). Thus, the Zambezian phytochorion can be seen as an evolutionary laboratory that promoted the evolution of many specialised plant species, e.g. geoxyles, orchids and grasses.

Geoxyle grasslands are sometimes misunderstood as ‘degraded forests’, overlooking their naturalness. Through this misconception they are listed as sites for reforestation in order to recover presumably lost forests and to sequestrate atmospheric CO_2 (Parr et al. 2014). However, the well-intentioned act of reforestation would in fact destroy biodiverse natural ecosystems (Bond 2016). A lack of understanding, however, frustrates the development of appropriate conservation measures for the geoxyle grassland today and in the future. The rebuilding process in Angola also has risks, happening at a rapid pace and shaping the landscape to human demands with limited consideration for sustainable management (Pröpper et al. 2015). Flooded savannas in the Moxíco Province for instance are targeted for largescale agro-industrial development (ANGOP 2017). Not even National Parks offer adequate protection to ecosystems in this area, as the first rice schemes emerged during 2016 within the limits of Cameia National Park (own observation). Deficiencies in communication and cooperation between different ministries and governance levels aggravate such problems.

Outlook

Many questions still remain to be answered around the enigmatic life form of the geoxyles. In order to effiiently safeguard geoxyle grasslands, we need to understand the evolutionary drivers and evolutionary processes shaping these ecosystems. For instance, a thorough understanding of the evolutionary drivers and the response of geoxyles to them would help to assess how current environmental conditions affect the Zambezian ecosystems and how landscape shaping processes work. Moreover, investigations about genetic patterns of geoxyle and close tree relatives would give insight to speciation processes, means of propagation (clonal or sexual) and evolutionary history. Also, ecophysiological or morphological measurements would contribute another perspective from which to assess how geoxyles react to environmental stresses and change processes. All these facets are currently the subjects of incipient research.

CHAPTER 3- Suffrutex grasslands in south-central Angola: belowground biomass, root structure, soil characteristics and vegetation dynamic of the “underground forests of Africa”

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Abstract

Despite its importance for many vegetation types, ecosystems and land-use systems, below-ground biomass so far has seldom been measured due to methodological complexity, the high effort, and the costs involved. This study assessed woody belowground biomass and related carbon stocks, soil properties and human impact of sandy *Parinari capensis*- and ferralitic *Brachystegia russelliae*-grasslands on the central Angolan plateau. MODIS remote sensing products on EVI and Fire were retrieved via Google Earth Engine, biomass and soil data were taken from plots using direct destructive sampling. Soil samples were analysed for a small set of selected key parameters. Both grassland types differ strongly in EVI and fire-seasonality. *Brachystegia russelliae*-grasslands have all year round a considerably higher EVI than *Parinari capensis*-grasslands, while these burn almost twice more frequent than *Brachystegia russelliae*-grasslands. All soils were extremely acid, showing a low nutrient availability. Most woody below-ground biomass is located in the top 30 cm of the soil. Mean below-ground woody biomass was estimated at 17 t/ha in sandy *Parinari capensis*-grasslands and 44 t/ha in ferralitic *Brachystegia russelliae*-grasslands of which 50% correspond to carbon stocks. We conclude that below-ground biomass in geoxylic grasslands is an important component for carbon stock accounting of African dry-tropical ecosystems.

Key words: Angola, belowground biomass, *Brachystegia russelliae*, carbon stocks, EVI, grassland fire, geoxyles; miombo, *Parinari capensis*.

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. 2013). 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. 2011). 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).

Material and Methods

Research site

The study was conducted in the Cusseque area of the Chitembo Municipality in Bié Province, Angola (Figure **7**). 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*).

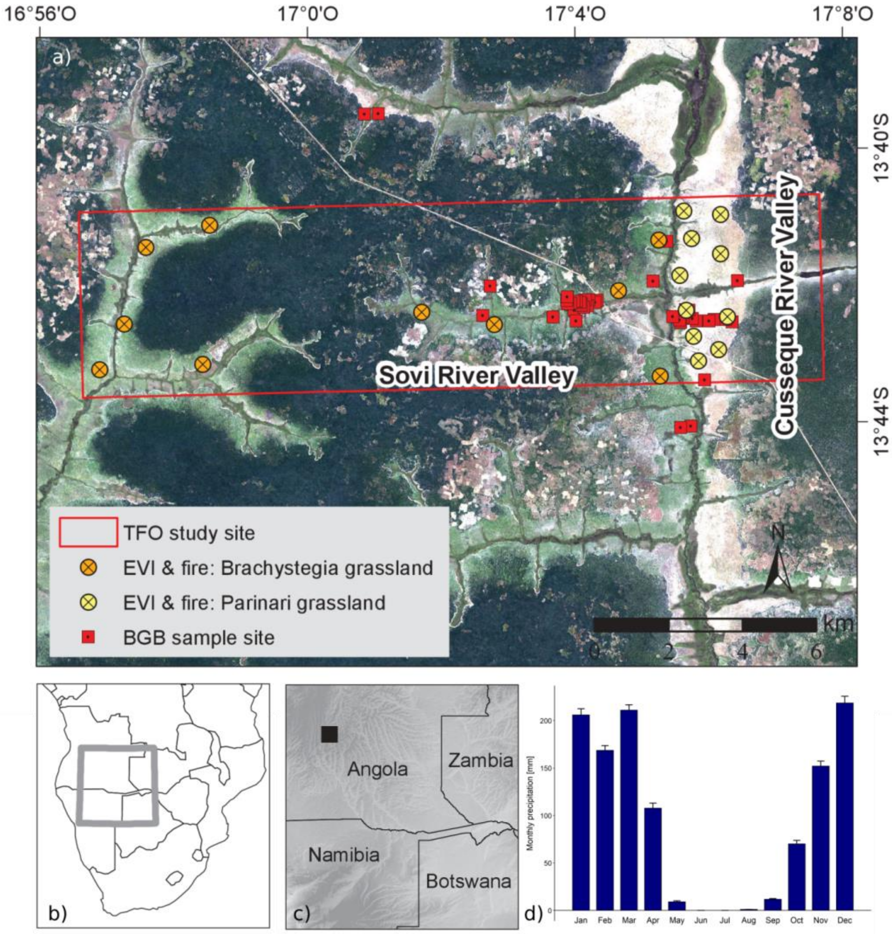

Figure 7: a) The research site Cusseque of The Future Okavango (TFO) project (www.future-okavango.org) in the upper Cubango basin (red rectangle, 100 km2). The occurrence of open suffrutex grasslands on ferralitic soils (light green color, e.g. in the Sovi River valley) and sandy deposits (white, eastern 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).

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 and Finckh 2013; Finckh et al. 2016).

Data collection

Seasonal vegetation dynamics of geoxylic 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 above ground biomass throughout the season we calculated the mean annual course of the EVI for both vegetation types over the ten 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. & 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. & T. DURAND. We excavated five individuals of each species. During excavation we carefully removed the soil around the individuals with 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 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. & Brenan does not fullymatch the description in Flora Zambesiaca. Specimen 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 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

Belowground biomass (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 two 1,000 m^2 (20 m x 50 m) plots divided into 10 sub-plots of 10 m x 10 m each; for each sub-plot we dug three pits of 0.5 m x 0.5 m x 0.5 m (length, width and depth) diagonally, with two pits in the opposite corners and one in the centre (Dengler 2009) as shown in Figure 8.

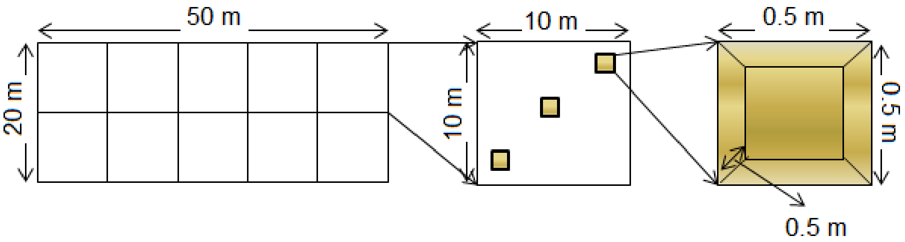

Figure 8: Sampling design of BGB within a 1000 m^2 plot subdivided in ten 100 m^2 subplots containing three soil pits (Adapted from Dengler 2009).

Furthermore, 48 pits (36 in *Brachystegia*-grasslands and 12 in *Parinari*-grasslands) of the same size were located in 16 plots of 10 m x 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 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 Moderate Resolution Imaging Spectroradiometer (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 ten year period from 2010 to 2019, we calculated for both vegetation types the seasonal mean monthly fire incidence per plot.

Data analysis

One-way ANOVA was used to test for significant differences of 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 geoxylic 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 lowest values observed in July, corresponding to the peak of the dry season, a marked increase in September already prior the onset of the rainy season, and the peak in December and January (Figure 9).

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 9).

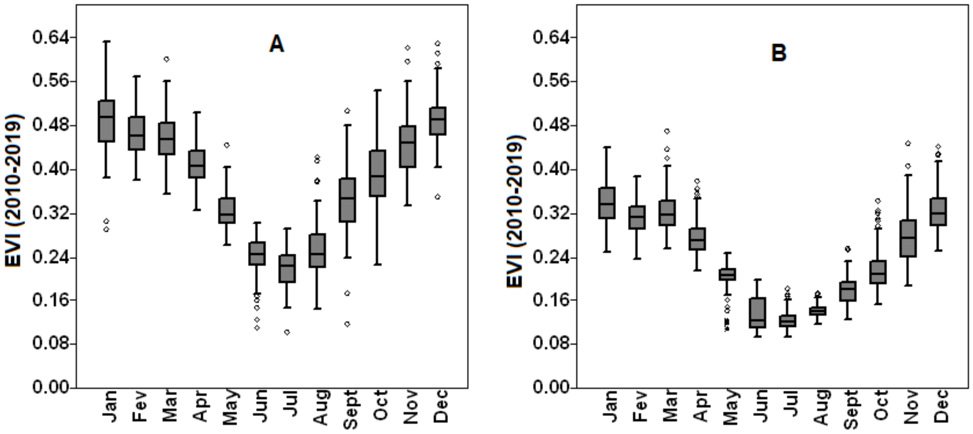

Figure 9: Annual phenology of *Brachystegia*- (A) and *Parinari*- (B) grasslands in the Cusseque study site on the Angolan central plateau. The graph shows monthly mean EVI values of a ten year observation period (2010-2019) for 20 systematically selected sample plots. Data was derived from the combined MYD13Q1 and MOD13Q1 data products via Google Earth Engine.

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 2). However, all species showed belowground bud banks (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 2 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. Examples of the underground organs of the studied species are shown in the Figure 10.

Table 2: 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[1]	woody rhizome	woody rhizome	lignotuber	woody rhizome	woody rhizome	woody rhizome
Growth direction	horizontal, interwoven, 2 layers	horizontal, interwoven, up to 4 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

[1] according to the classification by Pausas et al., 2018

Figure 10: The six geoxyle species discussed in the text, four of them with top-soil 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*.

Below-ground 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 S6, S7 and Figure 11). One-way ANOVA showed that BGB in *Brachystegia*-grasslands was significantly higher than in *Parinari*-grasslands (F=25; p<0.001).

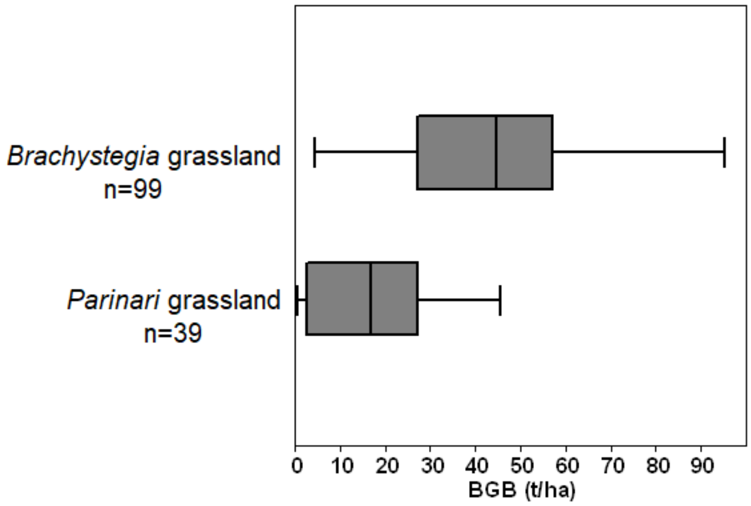

Figure 11: Box-whisker plots showing the range of BGB in *Brachystegia russelliae*- and *Parinari capensis*-grasslands).

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 exchangeable bases (K, Mg and Ca) and base saturation (V), very low cation exchange capacity (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 S3 and S4).

Comparing the two grassland-types (Table 3), one-way ANOVA revealed significant differences in soil properties: Sand content and pH_{KCl} were higher in *Parinari*- than in *Brachystegia*-grasslands, while pH_{CaCl_2}, 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 S3 and S4).

Table 3: 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	Std error	mean	Std error	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

Human impact on geoxyle 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 ten 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 two out of three years while *Brachystegia*-grasslands burn only (a bit more than) once in three 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*-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 12).

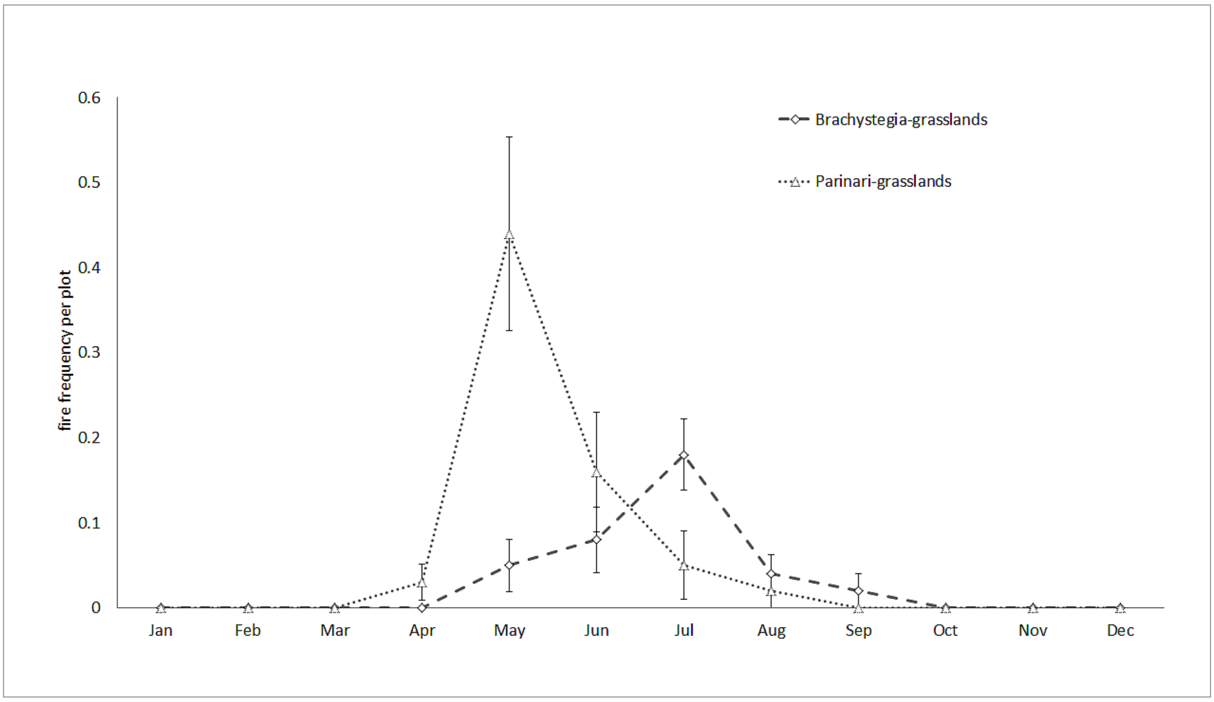

Figure 12: Mean monthly number of fires per plot over the 10 year period from 2010 to 2019 for *Parinari capensis*- and *Brachystegia russelliae*-grasslands in the study area (10 sample sites per vegetation type, based on the MODIS MCD64A1 Burned Area data product).

Some geoxyle species (e.g. *Syzygium guineense*, *Landolphia gossweileri* (STAPF) PICHON, *Anisophyllea fruticulosa* ENGL. & 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.

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 six 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 resemble closely 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.

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 belowground bud banks (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 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 among 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 among 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 to 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) up to 206.3 t/ha (maximum in Douglas fir forests) (Table 4). The BGB recorded for the suffrutex grasslands in central Angola amount to similar values recorded in other grassland and tropical savanna ecosystems (Table 4). 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 above ground biomass of the neighbouring woodlands.

Table 4: Global compilation of data on BGB for different vegetation types.

BGB t/ha)	Vegetation type	Country	Reference
16.0 to 37.0	Grassland	Szech Republic	Fiala 2011
44.6 to 49.4*	Grassland	USA	Fiala 2011
7.0 to 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 to 206.3	Upland Forest	global data	Cairns et al. 1997
7.0 to 52.0^{+}	Savanna	global data	Grace et al. 2006
1.1 to 17.0	Woodland (Miombo)	Mozambique	Ryan et al. 2011
16.3 to 52.9	Savanna/woodland (Brazilian cerrado)	Brazil	De Castro & Kauffmann 1998
21.4 to 29.5	Savanna	Brazil	Barbosa et al. 2012
17.8	Grasslands	Brazil	Miranda et al. 2014
33.6	Shrublands	Brazil	Miranda et al. 2014
17.8	Forestlands	Brazil	Miranda et al. 2014
6 to 7	Wet grasslands	Brazil	Fidelis et al. 2013
16.9-43.5	Rangeland	Nepal	Limbu & Koirala 2011

* data include dead BGB; $^{+}$ modelled data

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 for 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 $CaCl_2$), 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 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 geoxylic 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., 2013). 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 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 similarly 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 theses ecosystems are much higher than in neighbouring miombo woodlands and, in the case of *Brachystegia*-grasslands, are almost as high as values for above ground 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.

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CHAPTER 4- Tree or not a tree: differences in plant functional traits among geoxyles and closely related tree species

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Abstract

Geoxyles and their congeneric tree species are a very common feature in the Zambezian Floristic Region, however, little is known about differing expression of plant functional traits between the two life forms and thus their evolutionary adaptations to prevailing habitat conditions. Therefore, we measured selected plant functional traits and compared them between the geoxyle and tree growth forms. We selected six species pairs that are common in the study area, i.e. *Brachystegia russelliae* vs. *Brachystegia longifolia* (Fabaceae Detarioideae); *Cryptosepalum exfoliatum* subsp. *suffruticans* vs. *Cryptosepalum exfoliatum* subsp. *pseudotaxu*s (Fabaceae Detarioideae); *Combretum platypetalum* vs. *Combretum zeyheri* (Combretaceae); *Parinari capensis* vs. *Parinari curatellifolia* (Chrysobalanaceae); *Syzygium guineense* subsp. *macrocarpum* (suffrutex form vs. tree form) (Myrtaceae); *Uapaca nitida* var. *suffrutescens* vs. *Uapaca nitida* var. *nitida* (Phyllanthaceae). For analysis we selected traits reflecting adaptations to environmental conditions such as specific leaf area (SLA), leaf thickness (LT), wood density (WD), leaf nitrogen (LN), leaf carbon (LC), leaf phosphorus (LP), leaf calcium (LCa), leaf magnesium (LMg), leaf potassium concentrations (LP) and leaf dry matter content (LDMC). Additionally, we measured leaf water potential (WP) during dry and wet seasons. The results did not show a general pattern of inter life-form trait variation among trees and geoxyles. There were significant differences in LA, WD, LN, LC, LMg and LK between geoxyles and trees, but mostly among species pairs. This indicates that the growth form transition is largely decoupled from leaf economics. Thus, the detected differences in plant functional traits among the species pairs are mostly taxon related responses to specific environmental stresses and habitat conditions.

Keywords: Zambezian Floristic Region; Miombo; Geoxyles; Geoxylic suffrutex; Plant functional traits; Angola.

Introduction

The Zambezian Floristic Region is a diversity hotspot of ‘geoxyles’ (Simon and Pennington, 2012) in Africa. Geoxyles (also termed ‘geoxylic suffrutices’ (White, 1983) are widely distributed on the Kalahari sand deposits of the Upper Zambezi basin and within miombo ecosystems in Barotseland and southern Democratic Republic of the Congo (DRC) and Central Angola (White, 1983). Miombo woodlands (dominated by the genera *Brachystegia*, *Cryptosepalum*, *Isoberlinia* and *Julbernardia* from the Fabaceae subfamily Detarioideae) cover about 47% of Angola (Barbosa, 1970), mainly on the Angolan Central Plateau. However, these woodlands are broken up systematically by extended grasslands generally on lower slopes and valley floors, the so called ‘anharas de ongote’ or ‘anharas de borracha’, that harbour a high diversity of geoxyles.

Geoxyles are characterised by the reduction of perennial aerial stems and branches in favour of low, annual shoots protruding from disproportionally high underground woody biomass in the form of rhizomes or roots (Shaw, 1947). According to White's definition, each geoxyle can be paired with a congeneric tree counterpart, frequently in miombo woodlands (Burtt Davy, 1922; White, 1976). Beyond south-central Africa, they constitute a conspicuous feature of the campos cerrados of the Planalto of Central Brazil and similar growth forms occur as well in arctic alpine tundra environments in genera like Salix and Betula.

Geoxyles were mentioned in early botanical literature (Schimper, 1898; Warming, 1908) but discussions on the evolutionary drivers of the geoxylic life form are still ongoing. Environmental factors such as fire, frost, edaphic conditions and herbivory have been proposed as key drivers (Barbosa, 1970; Burtt Davy, 1922; Lamont et al., 2017; Steenkamp et al., 2001; White, 1976). Barbosa (1970) suggested geoxyles may be the result of strong fluctuations in soil water availability, associated with shallow hydromorphic soils, and low temperatures. Recently, studies conducted by Maurin et al. (2014) pointed at the interaction of fire frequency and high precipitation as main evolutionary drivers of the geoxylic life form. Finckh et al. (2016), in studies conducted in Angola, contradicted their point of view and proposed frost as the key driver of the evolution of geoxyles. Lamont et al. (2007) in a study on *Protea* species, stated that fire acted prior to frost in the evolution of the geoxylic life form.

Originating in most cases from tree ancestors starting in the late Miocene (approx. 10 Ma), the radiation of geoxyles reached a peak in the early Pleistocene (approx. 2.3 Ma) (Maurin et al., 2014). The speciation process has led to differentiation of trees and geoxyles into distinct taxonomic levels: there are cases where pairs of geoxyles and trees occur within subspecies, between subspecies, and between species. Finally, in some cases the level of differentiation is simply so far unknown, as floristic exploration and taxonomic studies of the Zambezian flora are still incomplete.

As geoxyles and tree life forms generally occur in contiguous but different habitat types (grasslands versus woodlands or forests), interactions between physiological and morphological traits may play a crucial role in explaining their evolutionary adaptations. ‘Plant functional traits’ are defined as morphological, physiological or phenological features measured at the individual level that impacts fitness (Violle et al., 2007).

Despite the stunning morphological similarities shown by many pairs of closely related geoxyle and tree species, few studies have examined the divergence of functional traits between the two growth forms. So far, studies investigating functional traits of plant species of the geoxylic grasslands of the Zambezian Floristic Region and the miombo ecosystems in general are rare (Chidumayo, 1994; Ernst and Walker, 1973; Ernst, 1975; Vinya et al., 2012). Meerts (2017) addressed the question of a diverging trait space of geoxyles and trees in Katanga, DRC, by analysing 7 morphological traits of 35 congeneric pairs obtained from standard floras. He found nested similarities in reproductive and vegetative traits. Hoffmann et al. (2005) found differences in leaf traits between savannah and forest trees in Cerrado vegetation in south-central Brazil.

Considering the specific environmental conditions prevailing in the habitats of geoxyles and trees, we hypothesise that the expression of plant functional traits of geoxyles in comparison to their tree counterparts differs and it is related to different physiological adaptation strategies to cope with environmental stresses. This study aims (1) to identify general differences in the trait space among the two life forms; (2) to describe differences in plant functional traits between congeneric pairs of geoxyles and trees; and (3) to identify adaptive traits of each life form to cope with environmental conditions of their respective habitats.

Material and methods

Research site

The study was conducted in the Cusseque area of Chitembo Municipality in Bie Province, Angola (Figure 13). The landscape of the study area is dominated by miombo forests on the hills and open geoxylic grasslands in the valleys. Altitude varies from 1397 to 1562 m. Predominant soils are either ferrallitic or sandy (Revermann et al., 2013).

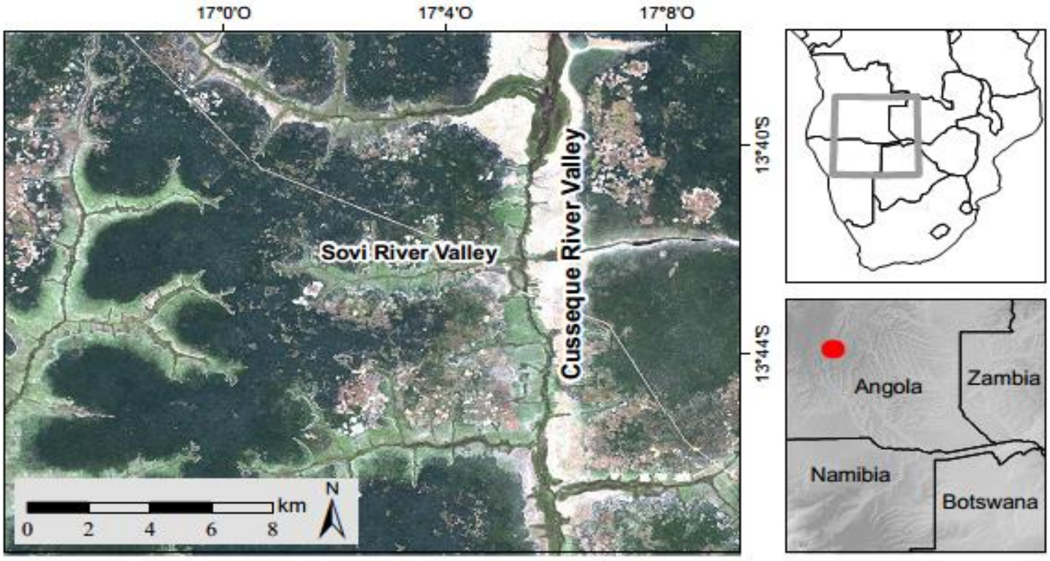

Figure 13: Location of the study area in Chitembo Municipality on the Angolan Central Plateau. The occurrence of open geoxylic grasslands on ferralitic soils (light green colour) and sandy deposits (white) is a characteristic feature in the valleys, contrasting with the forests on the hills (dark green).

The study area has a semi-humid 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 winter (June and July) especially in the valleys (Revermann and Finckh, 2013).

Species selection and study species

As the divergence between geoxyles and trees occurs at different levels in the various taxonomic groups, we selected cases for geoxyle tree pairs (a) within subspecies, (b) between subspecies, (c) between species, and (d) between subspecies and varieties (Table S1; Fig. S1 a-u). We attributed acronyms for each genus as follows: *Brachystegia* (B), *Cryptosepalum* (Cr), *Uapaca* (U), *Parinari* (P), *Syzygium* (S) and *Combretum* (Cb).

Trait sampling

We collected samples of all species pairs in early March 2014 near the peak of the growing season in close proximity to each other. All taxa are common in the study area, appearing well adapted to the local environmental conditions. Of each geoxyle and tree taxon five individuals fully exposed to the sun were selected for sampling. The geoxyles *Parinari capensis* and *Combretum platypetalum* were collected on sandy soils at the main Cusseque valley (North south oriented, white areas in Fig. 1), whereas all others taxa were sampled on ferrallitic soils of the Sovi tributary (west east oriented, light green areas in Fig. 1).

Measurements of plant functional traits

We selected plant traits known to show responses to a broad range of environmental factors and with a link to eco-physiological mechanisms well supported in literature (Kattge et al., 2011; Moles, 2018). For all species, we measured specific leaf area (SLA), leaf thickness (LT), leaf area (LA), wood density (WD), leaf carbon (LC), leaf nitrogen (LN), leaf phosphorus (LP), leaf calcium (LCa), leaf magnesium (LMg), leaf potassium (LK) concentrations and leaf dry matter content (LDMC). For five species we measured leaf water potential (LWP). Measurement of traits followed standardised protocols (Cornelissen et al., 2003; Muller, 2014; Perez-Harguindeguy et al., 2013)

SLA (LA/LDM)

For each species, 10 young leaves were collected from each of the 5 individuals. Each leaf (excluding petioles) was scanned with a portable scanner to determine leaf area (LA). Subsequently, the leaves were placed in a paper envelope and dried in an oven at 70 °C for 48 h until constant weight was achieved. Then we determined the leaf dry mass (LDM) using a high precision digital Kern 770 scale. LA for the scanned images was determined using XnViewMP software (available at: http://downloads.tomsguide.com/XnViewMP). For compound leaves we used only the leaflets, excluding the petiole and/or rachis.

LT

Ten leaves of five individuals (totalling 50 leaves per species) were collected following the same procedures as for SLA. The measurements were made using digital callipers at an intermediate position between the leaf margin and the midrib for each leaf. These individual measurements were then averaged to calculate mean values per species.

WD

For the geoxyles we collected woody samples (Diameter 2 cm) by digging up woody parts located belowground. For related tree species we collected branches with the same diameter size. To measure wood density we used the volume displacement method (Osazuwa-Peters and Zanne, 2011). After drying the woody segment in an oven at 103 °C for at least 72 h, we measured the weight and calculated WD (ratio of the dry mass and the fresh volume). Values were averaged per species.

LN and LC

Dried samples were ground finely with a disc mill (from Retsch solutions) and kept dry in an exsiccator. 100 200 mg of grounded material was then used for analysis in a Vario Max Cube Elemental C/N Analyser following the Dumas Combustion Method (Muller-Landau, 2004).

LP, LCa, LMg and LK

About 250 mg of dry leaf matter, finely ground, was digested with 8 ml of concentrated HNO3 plus 800 ml H2O2 in a tightly closed Teflon tube in a microwave (1600 W) for 15 min with a temperature ramp to 200 °C and heating for a further 15 min at 200 °C under pressure.

The resulting product was diluted in 50 ml of distilled water. Before measurement of all of these parameters in the ICP-OES (Spectro Arcos) all samples were centrifuged to precipitate any particles.

Before each run, a calibration was conducted with solutions of known concentration (0.0, 0.5, 1.0, 5.0, 10.0, 50.0 mg P/L) and a linear regression was fitted between P-concentration and signal intensity.

The ICP simultaneously measures signals (spectra) that were created by passing ionising Argon plasma at different wavelengths, with each wavelength characteristic for an element or ion. For P, seven wavelengths were measured and signals from Ca, K and Mg wave lengths were recorded as well. The signals of all elemental specific wavelengths were averaged (except when a wavelength gave deviating signals, in which case it was excluded; for this reason only five spectral lines were used for averaging P). Furthermore, the spectra were examined thoroughly to detect any interfering signals or background/underground disturbance. In such cases the errors were corrected and concentrations recalculated.

LDMC

Because water-satured fresh leaf mass was not measured in the field, LDMC was estimate indirectly from the following equation: LDMC 1/(SLA x LT) (Perez-Harguindeguy et al., 2013). Prior to calculation, values of LT were divided by 10 to achieve the same units as in SLA (cm).

LWP

Measurements were made under field conditions using a pressure Pump-Up Chamber Instrument (PMS Instrument Company USA), a methodology first described by Scholander et al. (1965). Measurements were made twice a day in the rainy season (end of March) and in the dry season (early June), just before dawn (5 6 am) and at noon. Five leaves per species from five different individuals were successively cut and placed inside the chamber, with the cut end protruding from the seal. Pressure was gradually increased until a water film appeared on the cut. Then, pumping was stopped and the pressure recorded. It was not possible to measure LWP of *Combretum platypetalum* in the dry season because this species is deciduous and sheds its leaves early. For this reason, we excluded the pair of *Combretum* species when analysing data for LWP. Due to pressure limitations of the pump, we regarded the pump's maximum pressure (21 bar) as LWP for those species where no sap flowed at the cut surface. However, the real values were more negative than 21 bar indicating high water stress.

Data analysis

Principal components analysis (PCA) was used to examine relationships between the groups and among traits simultaneously based on the correlation matrix of variables. PCA was also used to assess the relationship among species and traits simultaneously. Before calculating the PCA, variables were standardised in order to eliminate influence among the variables in the formation of components. Comparisons of all plant traits between the groups were made using a Two-way ANOVA with genera and life form as main factors and the interaction term of both. While a significant life form effect indicates a systematic difference of the tested trait among geoxyles and trees, a significant interaction term points at genus-specific differences among the two life forms. Tukey's LSD post-hoc test was used to identify significant differences within the pairs. Analyses were done using the statistical software R (R Core development team, 2017) using ‘vegan’, PAST (Version 2.16), and BioEstat (Version 2.0) packages.

Results

General patterns of correlation among traits

Principal component 1 (PC1) and 2 (PC2) together explained about 65% of the variance (Figure **14**). PC1 is associated with LP, SLA, LN, WD and LT, while PC2 is associated with LMg, LK, LCa and LC. PC1 clearly separates Fabaceae-Detarioideae (*Brachystegia*, *Cryptosepalum*) species having higher SLA and LN from the species with thick leaves, having a more efficient stomatic control to maintain water potential.

PC2 separates the Fabaceae Detarioideae into geoxyles and trees as well. Geoxyles have higher LCa, LMg and WD, while respective trees have higher LN.

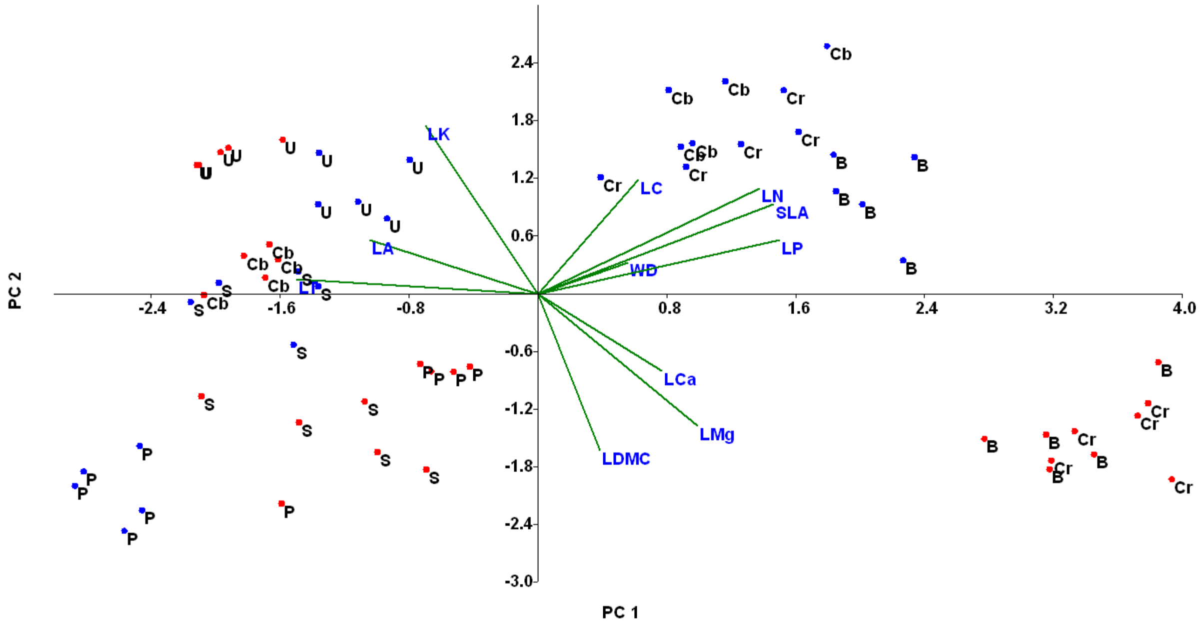

Figure 14: PCA showing the relationship among species, plant traits and life form. Geoxyles (red circle) and trees (blue circles) include B, *Brachystegia*; Cr, *Cryptosepalum*; U, *Uapaca*; P, *Parinari*; S, *Syzygium*; Cb, *Combretum*.

Trait differences among the two life forms: Inter-life-form variation

Seven of the eleven plant traits varied among the two life forms (geoxyles and trees). Two-way ANOVA (Tables 5 and 6) showed significant differences in LA, WD, LN, LC, LMg, LK and LWP among geoxyles and trees. On average geoxyles had denser wood and higher LMg than trees while LA, LN, LC and LK were higher in trees than in geoxyles.

Table 5: Results of a two-way ANOVA of all plant traits with the factors life form, genera and the interaction term of both; significant differences are marked in bold.

Trait	Mean geox.	Mean trees	Two-way ANOVA (α=0.05)			
			-	Inter life form	Inter genera (pairs)	interaction life form: genera
SLA (cm^2 g^{-1})	81.66	82.89	F	0.49	52.66	15.46
			p-value	0.49	**0.000**	**0.000**
LT (mm)	0.2995	0.2996	F	0.0017	277.3	82.02
			p-value	0.967	**0.000**	**0.000**
LA (cm^2)	83.20	97.38	F	16.08	231.85	7.63
			p-value	**0.000**	**0.000**	**0.000**
WD (g cm^{-3})	0.6226	0.5457	F	12.45	5.72	1.04
			p-value	**0.000**	**0.000**	0.405
LN (%)	1.552	1.725	F	22.38	110.9	32.52
			p-value	**0.000**	**0.000**	**0.000**
LC (%)	48.97	49.87	F	4.48	45.91	10.69
			p-value	**0.039**	**0.000**	**0.000**
LP (mg g^{-1} tissue)	1.033	1.083	F	2.35	63.69	27.06
			p-value	0.132	**0.000**	**0.000**
LCa **(**mg g^{-1} tissue)	4.89	5.53	F	3.79	8.84	25.46
			p-value	0.057	**0.000**	**0.000**
LMg (mg g^{-1} tissue**)**	2.64	0.31	F	108.08	26.94	23.41
			p-value	**0.000**	**0.000**	**0.000**
LK (mg g^{-1} tissue)	5.88	9.97	F	1128.97	138.65	243.08
			p-value	**0.000**	**0.000**	**0.000**
LDMC (mg g-1 tissue)	0.44	0.43	F	2.10	55.76	8.29
			p-value	0.154	**0.000**	**0.000**

Trait differences among species pairs of geoxyles and trees: Interpair variation

In the ANOVA the interaction term of life form and genera was significant in all traits except in wood density, indicating a genus specific response. As such, the pairwise comparison based on Tukey LSD showed inter-pair trait variation in all plant traits (Table 6). In some plant traits the variation was in only one pair (e.g. WD), while in others it was in all pairs (e.g. LT and LCa).

Table 6: Inter-pair trait variation based on Tukey LSD pairwise comparison. Significant differences were obtained comparing absolute value of the mean difference (AMD) of each pair with least significant difference (LSD) (AMD<LSD: there are no differences; AMD>LSD: significant differences). Significant differences are marked in bold. B = *Brachystegia* pair; Cr = *Cryptosepalum* pair; U = *Uapaca* pair; P = *Parinari* pair; S = *Syzygium* pair; Cb = *Combretum* pair.

Traits	Absolut value of the mean difference between pairs (AMD)						LSD value
	B	Cr	U	P	S	Cb	
SLA	5.380	**13.692**	1.561	**18.099**	2.343	**29.906**	8.720
LT	**0.016**	**0.054**	**0.048**	**0.119**	**0.053**	**0.055**	0.0159
LA	12.65	2.760	15.382	**46.84**	5.240	**38.020**	17.524
WD	**0.125**	0.072	0.067	0.087	0.018	0.063	0.108
LN	0.160	**0.184**	0.077	**0.307**	**0.209**	**1.137**	0.182
LC	1.775	**5.737**	0.712	**4.651**	0.195	1.993	2.095
LP	0.106	**0.399**	**0.318**	**0.170**	0.096	**0.753**	0.161
LCa	**4.446**	**4.444**	**2.770**	**3.502**	**1.953**	**4.471**	1.612
LMg	**4.229**	**2.773**	0.064	0.034	**4.436**	0.151	1.114
LK	**8.698**	**8.172**	0.142	**0.930**	**8.075**	0.399	0.604
LDMC	0.008	**0.051**	**0.039**	**0.045**	**0.053**	**0.066**	0.035

In the following we consider significant differences of each trait separately. The symbol g < t or g > t indicates that the *geoxyle* trait is lower or higher than the tree trait, respectively.

SLA

Overall, SLA did not vary significantly between geoxyles and trees (p>0.05). Two-way ANOVA showed significant differences between genera and also significant interaction between life form and genera (p<0.05), indicating genus-specific differences between the two life forms. Tukey's LSD pairwise comparison detected differences in three pairs: *Cryptosepalum* (g>t), *Parinari* (g>t) and *Combretum* (g<t).

LT

In general, LT did not vary significantly between geoxyles and trees (p>0.05). Two way ANOVA showed significant differences between genera and also significant interaction between life form and genera (p<0.05), indicating also genus-specific differences between two life forms. However, Tukey's LSD pairwise showed significant differences in all pairs studied (*Brachystegia*, *Uapaca*, *Syzygium* and *Combretum*: g>t; *Cryptosepalum* and *Parinari*: g<t).

LA

In spite of the significant differences between geoxyles and trees, between genera and also significant interaction between life form and genera (p<0.05), Tukey's LSD only found significant differences in *Parinari* and *Combretum* (both g<t).

WD

Two way ANOVA showed significant differences between geoxyles and trees and between genera (p<0.05) but no significant interaction between life form and genera. Tukey LSD pairwise showed differences only in the *Brachystegia* pair (g>t).

LN

There were significant differences between geoxyles and trees, between genera and also significant interaction between life form and genera (p<0.05). LN was higher in trees than in geoxyles. Tukey LSD pairwise detected differences in the pairs *Cryptosepalum* (g<t), *Parinari* (g>t), *Syzygium* (g>t) and *Combretum* (g<t).

LC

Similarly, there were significant differences between geoxyles and trees, between genera and significant interaction between life form and genera p<0.05). LC was higher in trees than in geoxyles. Tukey LSD pairwise showed differences in two pairs namely *Cryptosepalum* (g<t) and *Parinari* (g>t).

LP

Significant differences were found between genera and there was also significant interaction between life form and genera p<0.05). Tukey LSD pairwise detected differences in the pairs *Cryptosepalum* (g>t), *Uapaca* (g<t), *Parinari* (g>t) and *Combretum* (g<t).

LCa

There were significant differences between genera and significant interaction between life form and genera (p<0.05). Tukey LSD pairwise detected differences in all pairs (*Brachystegia* and *Cryptosepalum*: g>t; *Uapaca*, *Parinari*, *Syzygium* and *Combretum*: g<t).

LMg

There were significant differences between geoxyles and trees, between genera and there was significant interaction between life form and genera (p<0.05). Meanwhile Tukey LSD pairwise only detected differences in three pairs namely *Brachystegia*, *Cryptosepalum* and *Syzygium* (for all, g>t).

LK

There were significant differences between geoxyles and trees, between genera and there was significant interaction between life form and genera (p<0.05). Tukey LSD pairwise detected differences in four pairs namely *Brachystegia*, *Cryptosepalum*, *Parinari* (for all, g>t) and *Syzygium* (g<t).

LDMC

ANOVA did not show any differences between the two life forms (p > 0.05), however, the signficant interaction term indicates genus-specific differences. This becomes evident in the pairwise comparison (**Table 6**): five out of six showed significant differences. The boxplots (**Figure 15**), however, show an inconsistent pattern. In two cases the trees have significantly lower LDMC (U, S) and in three (Cr, P and Cb) the geoxyles do. Figure 15 illustrates all traits among the pairs of geoxyles and trees.

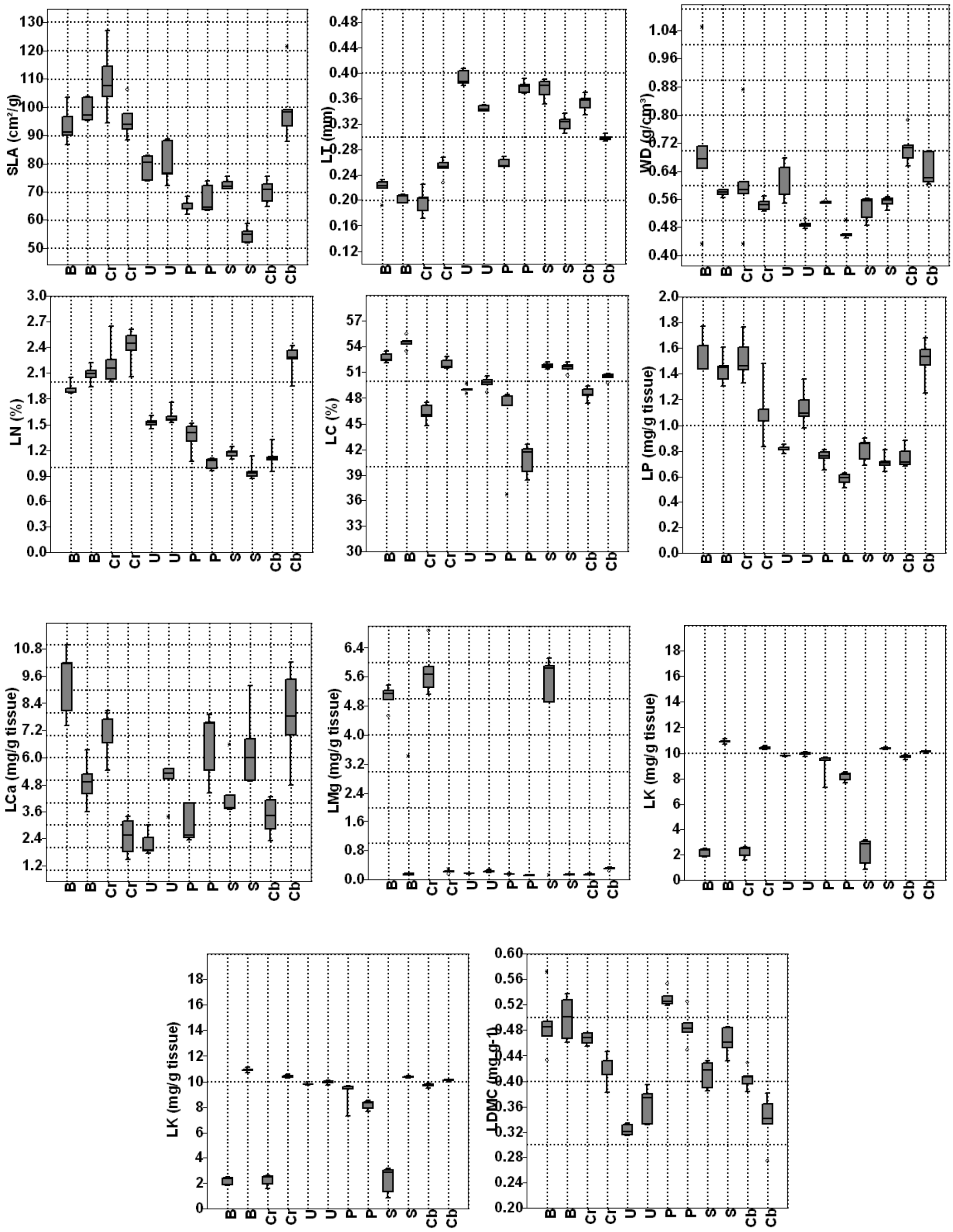

Figure 15: Boxplots depicting the mean values of traits for pairs of geoxyles and trees for the 6 genera. B- *Brachystegia*; Cr- *Cryptosepalum*; U- *Uapaca*; P- *Parinari*; S- *Syzygium*; Cb- *Combretum*.

LWP

There were significant differences among the two life forms before dawn in the rainy season (p<.05). At midday of the same season there were also significant differences among life form, between genera and interaction (p<.05). However, no significant differences were detected among life forms (p>.05) before dawn in the dry season but there were significant differences among genera (p<.05) indicating different plant strategies to cope with water stress. This can be seen in the high significance of interaction (p<.01). At midday in the dry season differences among life forms were significant, as well as between genera and significant interaction (p<.05). However, there were strong differences from predawn to midday and between seasons. Generally, there was low or no water stress at predawn, while plants experienced low to high water stress at midday and LWP showed significant variations from predawn to midday in both seasons ranging from 0 to less than -21 bars (Table 7). Some species pairs showed high water stress experienced by both life forms at midday. The degree of water stress severity varied according to species and to the strategy adopted by the plants to cope with water scarcity. The three large-leaved evergreen trees *Uapaca nitida*, *Parinari curatellifolia* and *Syzygium guineense* subsp. *macrocarpum* were seen to do considerably better than the corresponding geoxyles. At midday LWP varied between -15 and -6.9 bar, compared with much higher values for their *geoxyle* partners.

Table 7: Two-Way ANOVA of LWP (bar) comparing two life form (geoxyles and trees) measured in two seasons (rainy and dry) twice a day (predawn and midday). Significant differences are marked in bold.

Season	**period**	**Mean geox.**	**Mean trees**	**Two-way ANOVA (α=0.05)**			
				-	**sample**	**columns**	**interaction**
Rainy	Predawn (5h)	-0.11	0	F	5.98	0.012	0.012
				p-value	**0.019**	0.999	0.999
	Midday (12h)	-19.44	-14.5	F	64.87	46.33	14.81
				p-value	**0.000**	**0.000**	**0.000**
Dry	Predawn (5h)	-1.81	-1.52	F	3.17	8.26	5.89
				p-value	0.082	**0.000**	**0.000**
	Midday (12h)	-16.74	-12.8	F	80.18	177.75	17.32
				p-value	**0.000**	**0.000**	**0.000**

During the rainy season, among geoxyles, only *Uapaca nitida* var. *suffrutescens* did not show strong variation of water potential and consequently was less stressed than the other species. During the dry season, geoxyles showed slight water stress at predawn, with LWP ranging between -2.8 and -0.5 bars. At midday, the stress experienced by these plants was less severe than observed at the same period of the rainy season for most species. Only *Cryptosepalum exfoliatum* reached the maximum pump pressure (-21 bar) during the dry season. Among trees, at predawn of the dry season LWP ranged between -2 and -1 bars while at midday it ranged between -2.6 and -21 bars.

Discussion

Due to the limited sample size of the present study our results should not be extrapolated to apply to entire genera. Nevertheless, these results could constitute a base for future research.

Differences among the two life forms

While trees and geoxyles differ drastically in their growth form, they are remarkably similar in other morphological traits (Meerts, 2017). Yet, we found a general pattern of inter-life-form variation of traits in LA, WD, LN, LC, LMg and LK. None of the other traits showed a general pattern of inter-life-form variation. Within one taxonomic group, the Fabaceae Detarioideae, we detected significant differences between trees and geoxyles, which may indicate a certain phylogenetic conservatism in ecophysiological and functional traits. Thus, a main finding, considering the differences in traits among the two life forms, is the surprising inconsistency of responses among the different families.

Traits differing among the life forms were LA, WD, LN, LC, LMg and LK. In general, WD was higher in geoxyles than in trees. Lower WD tends to be associated with faster stem diameter and volumetric growth (Enquist et al., 1999; King et al., 2005; Muller-Landau, 2004; Roderick, 2000), however, it has never been systematically analysed for underground woody organs. Higher WD of geoxyles is associated with lower volume of xylem (Sanguino Mostajo, 2015). This may be related to less transpiring leaf biomass per shoot and thus lower demand for the corresponding hydraulic capacity (Ackerly, 2004; Bucci et al., 2004; Givnish, 1995; Loehle, 1988). However, higher WD decreases stem water storage (Ackerly, 2004; Bucci et al., 2004). Lower stem water storage and higher transpiration losses in the open grasslands may be two factors that contribute to the higher water stress in geoxyles than in trees.

LN was another trait that differed among life forms (trees had more LN than geoxyles). A high LN concentration is associated with increase of SLA and LP and decrease of LT and LA (see PCA). The relation between LN and SLA is in general linear (Schulze et al., 1994), playing both a key role in the rate of photosynthesis, as there is a close relationship with CO_2 assimilation rate. Two-way ANOVA results showed that trees in general had a higher SLA than geoxyles, indicating a higher rate of photosynthesis associated with efficient CO_2 assimilation.

LMg and LK are also two plant traits with significant differences among life forms (LMg: g > t; LK: g < t). Magnesium is very important in photosynthesis, being the central atom in the chlorophyll molecule and involved in many enzymatic reactions (Schwartzkopf, 1972; Tuma et al., 2004). Potassium plays a key role in the stomatal movements impacting the plant water balance (Hugouvieux et al., 2002). Lower K+ associated with Ca2+ deficiency in geoxyles could be related to their lower resistance to water stress (Seyed et al., 2012), as they activate leaf shedding and stomatal control earlier than the trees.

Differences in plant functional traits between the species pairs

For all analysed traits we found significant differences at least in some species pairs. As discussed above, the direction of these differences was not consistent among taxonomic groups. All pairs differed among life forms in LT and LCa while only the *Brachystegia* pair (g > t) differed in WD. While not differing significantly among life forms in general, SLA was different in three pairs: *Cryptosepalum* (g > t), *Parinari* (g > t) and *Combretum* (g < t). The general correlations among traits as shown in the PCA correspond to patterns observed in related studies (Douma et al., 2011; Wilson et al., 1999). SLA is known to be positively related to LN, LP, relative growth rate (RGR), leaf carbon assimilation rate and energy supply (Lambers and Poorter, 1992; Reich et al., 1992, 1997) and negatively related to LT (Poorter, 1990) and LDMC (Westoby et al., 2002). Our results showed a negative correlation between LT and LDMC and very weak correlation between SLA and LDMC. These results point to differences in terms of better light capture and gas exchange, as SLA, LN and LP are closely linked with leaf gas exchange (Evans, 1989; Field and Mooney, 1986). For *Cryptosepalum* and *Parinari*, SLA was higher for geoxyles than for trees. *C. exfoliatum* subsp. *suffruticans* and *P. capensis* are very low-growing geoxyles reaching a mean height of less than 5 cm. Thus, they are grassland understorey species that may need an efficient assimilation system to cope with shading. On the contrary, their tree counterparts are normally not shaded, such that the enhancement of assimilation efficiency at the cost of water efficiency (reduced leaf thickness) may not be an evolutionary priority. For *Combretum*, SLA, LN and LP of the geoxyles were much lower than the SLA of the tree partner *C. zeyheri*. As *C. platypetalum* emerges for the first half of the vegetation period from the ground layer, an inverse optimisation strategy may make sense.

Despite no difference among life form, LT and LCa varied considerably between genera. LT is negatively correlated with SLA, LN, LP and LDMC. Negative relationships between LT and photosynthetic rate (Enriquez et al., 1996; Garnier et al., 1999) and relative growth rate (Nielsen et al., 1996; Poorter, 1990) have been reported, and thicker leaves have been associated with increased longevity and construction costs (Mediavilla et al., 2001; Westoby et al., 2002). PCA (**Figure 14**) shows the negative correlation between LT and SLA, LN, LP and LDMC. Geoxyles that have thicker leaves showed lower SLA, LN, LP and LDMC, respectively, than their tree counterparts and vice-versa. Some of the taller geoxyles, like *Uapaca, Syzygium* and *Combretum*, have thicker leaves than their counterparts, indicating that they have to trade a lower photosynthetic rate and also a lower relative growth rate for improved water efficiency. Growing tall and exposed to the sun in the open grasslands, this trade-off is easy to explain. Consistent with this line of reasoning, for the lower growing and less exposed ‘grassland understorey species’ *Cryptosepalum exfoliatum* subsp. *suffruticans* and *Parinari capensis* the situation was reversed, with trees having the thicker leaves (see discussion on SLA above).

LMg tended to be higher in the *Brachystegia*, *Cryptosepalum* and *Syzygium* geoxyles than in their tree partners. Magnesium cannot be discussed separately from other nutrients, especially calcium and potassium, due to the antagonistic relation in uptake

(Tuma et al., 2004). Higher LMg in geoxyles could be a quick development strategy. After leaf shedding and early before the onset of the rainy season, these species resprout, grow, and start flowering and fruiting rapidly, before being covered by C4 grasses and other herbs in the later rainy season in January. Their tree counterparts keep their leaves over the dry season and renew them successively at the start of the next rainy season. This precocious development of these geoxyles is an ecological strategy, and must be associated with high photosynthesis rates and gas exchange, processes that are influenced by Mg and K concentrations (Peoples and Koch, 1979). The consistently lower LK in geoxyles may allow them to acquire Mg more easily (Tuma et al., 2004) for a quick development strategy.

Leaf nutrient concentrations reflect soil nutrient availability (Brockley, 2001) and also the capacity of the species to take up nutrients, e.g. via mycorrhiza, proteoid roots or symbionts. Soils of the Kalahari region are considered extremely poor in terms of nutrients (Frost, 1996). According to Groengroeft et al. (2013), the top soils of our study area have significantly lower nutrient contents than the lower soil horizons. Our results did not reflect this limitation and leaf nutrient contents of our samples correspond to the range of variation found in many cultivated plants (Uchida, 2000). This surprisingly high nutrient status of the natural flora could be partly attributed to translocation processes, phenomena that occur in most plants (Ackerly and Bazzaz, 1995; Nooden, 1988). Nutrient conservation through resorption is a main ecophysiological strategy adopted by many plants in nutrient-poor soils like in miombo woodlands (Chidumayo, 1994), allowing for nutrient recycling rather than loss with leaf fall. For *Cryptosepalum*, *Brachystegia* and *Uapaca*, however, the association to ectomycorrhizal fungi (Corrales et al., 2018) allowing for fast recycling of nutrients from litter may play an important role for their high nutrient status.

Comparable adaptation strategies to water stress among pairs of trees and geoxyles

The three broad-leaved evergreen trees *Uapaca nitida*, *Parinari curatellifolia* and *Syzygium guineense* subsp. *macrocarpum* maintained their water status over the day considerably more stable than the corresponding geoxyles. This suggests that these trees either have more efficient stomatal control or that they are favoured by more mesic microclimatic stand conditions compared to the sun-exposed geoxyles in the grasslands.

However, it was also interesting to observe that the broad-leaved evergreen species with higher LT and lower SLA in general, namely *Uapaca* spp., *Parinari* spp. and *Syzygium guineense* subsp. *macrocarpum*, showed a more efficient stomatal control than the other (partly deciduous) species in both seasons of the year, e.g. *Brachystegia longifolia* and *B.russelliae*. The higher the SLA, the more negative was the water potential. This indicates that the leaf construction cost is associated with water use efficiency (Mediavilla et al., 2001). However, it was also evident that LT was associated with leaf life span. Thicker leaves with more LDMC remain for a longer time on the plant and thus have to maintain water use efficiency or water potential over the dry season (Poorter and Bongers, 2006), while deciduous species can control their water losses by successive leaf shedding.

Adaptive traits

The results obtained in this study demonstrate that the pairs of *geoxyle* and trees, despite having different life forms, rather have similar (phylogenetically inherited) strategies to deal with drought. Each strategy adopted occurred first in geoxyles and then in trees (Table S1), maybe because they are more strongly exposed to climate related stresses. Two mechanisms were identified to cope with water stress: stomatal control and leaf shedding. While the broad-leaved evergreen taxa primarily use stomatal control, the *Brachystegia* and *Combretum* pairs primarily fall back on leaf shedding. However, according to the severity of drought, the species sequentially apply stomatal control before resorting to shedding their leaves.

The lower growth rate of the aerial parts of geoxyles seems to be an evolutionary adaptation to destructive above-ground processes like frost and fires in open grassland. High LMg in geoxyles indicates an intense photosynthetic activity. In the absence of light competition in the first half of the growing season, however, geoxyles tend to invest more strongly in belowground organs (stems, roots and/or storage organs) and in turn reduce the growth rate of aerial parts.

Finally, there were no significant overall differences in SLA between geoxyles and trees. The taxa have evolved different strategies to optimise the balance between assimilation rate and water losses according to their habitat niche.

Conclusions

This study is one of the first to analyse physiological differences between trees and their enigmatic diminutive counterparts, the geoxyles, based on plant functional traits. We show that there is no consistent shift in the phenetic space of geoxyles compared with closely related tree counterparts. There is no easy trait dualism between trees and geoxyles, but each taxon tends to optimise its evolutionary fitness in a multidimensional trait space according to its (phylogenetically inherited) eco-physiological pre-adaptations and the available environmental niche space.

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Supplementary materials

Supplementary data associated with this article can be found in the appendix of this thesis or in the online version, at DOI:10.1016/j.sajb.2019.08.044.

CHAPTER 5- Functional traits and symbiotic associations of geoxyles and trees explain the dominance of detarioid legumes in miombo ecosystems

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Summary

- The miombo region in Africa is covered by a mosaic of woodlands and geoxylic grasslands and subject to disturbances like fires, frost and drought, and low nutrient availability. The dominance of Fabaceae Detarioideae species in miombo ecosystems is remarkable but little understood. We therefore compared plant functional traits (PFTs) of common woody species of the Angolan plateau, grouped by life form (trees, geoxyles), lineage (Fabaceae: Detarioideae, non-Detarioideae) and symbiont association (ectomycorrhiza, rhizobia).
- PFTs reflect group-specific adaptations to prevalent environmental conditions. To analyse the impact of environmental drivers, we selected PFTs reflecting ecophysiological aspects of leaf morphology, nutrient content and water transport. Traits were measured following standardized protocols.
- We found differences in key PFTs between trees and geoxyles reflecting both, life form specific adaptations to environmental conditions and lineage specific strategies to cope with environmental stresses. We interpret higher leaf thickness and higher wood density of geoxyles as responses to harsher open environments. Fabaceae in general and ectomycorrhizal species showed better nutrient status.
- Symbiotic associations of detarioid legumes with ectomycorrhiza show specific advantages for phosphorous uptake as compared to Rhizobia associated Fabaceae and to non-Fabaceae and thus may be crucial for the stunning dominance of Detarioideae in miombo landscapes.

Key words: ectomycorrhiza; Fabaceae Detarioideae; geoxyles; geoxylic grasslands; Rhizobia; trait-based plant strategies; trees.

Introduction

The miombo ecoregion is one of the main biomes of south-central Africa covering more than 3.6 million km² across 11 countries including Angola (Chidumayo, 1995; Frost, 1996). Miombo ecosystems are typically dominated by woody plants from the genera *Brachystegia*, *Julbernardia*, *Isoberlinia* and *Cryptosepalum* (Frost, 1996; Timberlake & Chidumayo, 2011), belonging to the legume subfamily Detarioideae (LPWG, 2017).

In Angola, miombo woodlands correspond to approx. 47% of the total land area (Barbosa, 1970) and are the main vegetation type, covering the landscape of the Central Plateau. Generally, miombo woodlands form mosaics with open habitats along the valleys (Stellmes *et al.*, 2013 a). These open habitats are co-dominated by dwarf shrubs with massive underground woody structures (geoxylic suffrutices; White, 1976, Zigelski *et al.*, 2019; hereafter termed geoxyles) together with tall C4-grasses. These geoxylic grasslands are locally known as *Anharas* or *Chanas*.

Due to their ecological and socioeconomic importance (Campbell, 1996; Syampungani et al., 2009; Timberlake & Chidumayo, 2011; Sanfilippo, 2014) miombo woodlands have been subject of studies in many countries in the eastern miombo region (Williams et al., 2008; Shirima et al., 2011; Kalaba et al., 2012; Jew et al., 2016). In Angola, however, miombo woodlands have been less well-studied (e.g. Sanfilippo, 2014; Revermann et al., 2016, 2018; Goncalves et al, 2017).

The need to study the ecophysiology of miombo woodlands as a base for its sustainable management has been emphasized for more than two decades (Chidumayo, 1995; Campbell, 1996). Human population growth accompanied by land use change and intensification makes it urgent to better understand the stresscoping mechanisms of miombo vegetation. Miombo is subject to many environmental stresses such as generally low nutrient availability (Chidumayo, 1994; Frost, 1996), and fire (Ryan & Williams, 2011), frost (Finckh et al., 2016) and water stress (Vinya et al., 2012) in the dry season. Leaf shedding (Frost, 1996) by woody plants and underground allocation of assimilates and biomass by geoxyles (White, 1976; Zigelski et al., 2019) are conspicuous responses to these stresses. Nitrogen-fixing root nodules and mycorrhizal associations are less obvious and remain understudied in the western miombo region, although they are known to improve the ecophysiological fitness of plants in challenging environments (Malloch et al., 1980; Dakora & Phillips, 2002; Tedersoo et al., 2020).

Plant functional traits (PFTs) have been used as an approach to study ecophysiological responses of plants to a broad range of environmental factors which allows a better understanding of functional groups associated with resource use, life strategies and ecosystem functioning (Reich et al., 2003; Violle et al., 2007; Garnier & Navas, 2012; Perez-Harguindeguy et al., 2013). So far, some baseline studies on functional traits from savanna and forest ecosystems have included miombo ecosystems (Chidumayo, 1994; Hoffmann et al., 2005; Poorter & Bongers, 2006; Vinya et al., 2012). However, studies comparing traits from tree species in miombo woodlands with geoxyle species from the neighbouring geoxylic grasslands are still scarce (Meerts, 2017; Gomes et al., 2019).

Of specific interest in this context is the dominance of the legume subfamily Detarioideae in African tropical and subtropical forests (Estrella et al., 2017) (comprising miombo woodlands and associated geoxylic grasslands). Detarioid legumes are not associated with nitrogen-fixing Rhizobia (as is the case in most Fabaceae) but many genera have ectomycorrhizal (ECM) symbionts (Estrella et al., 2017). Corrales et al. (2018) suggest that ECM associations on nutrient-poor tropical soils optimize nutrient supply and thus might be pivotal for the dominance of ECM-associated taxa in many tropical forest ecosystems, especially among the families Dipterocarpaceae (Asia) and Myrtaceae (Australia). However, Corrales et al. (2018) indicate that grassland ecosystems have been poorly studied in relation to ECM occurrence and species composition. So far, no analysis has been made on how detarioid and nondetarioid legumes perform comparatively under woodland vs grassland conditions.

Thus, to better understand functional adaptations of woody taxa in grassland vs woodland habitats, we compare PFTs of geoxyles and trees co-occurring in contiguous miombo landscapes and discuss the role of environmental factors for the differences in PFTs. Then we investigate how far the differences in PFTs are influenced by lineage-specific symbiotic interactions in order to better understand why detarioid legumes are such a dominant element in miombo woodland as well as associated grassland habitats.

Material and Methods

Research site

The study was conducted in the Cusseque area of the Chitembo Municipality, located in Bié Province, Angola (Figure 16). The landscape of the study area is dominated by miombo woodlands on the hills and open geoxylic grassland in the valleys. Predominant soils are either sandy (Arenosols) or ferralitic (Plinthosols), characteristically very acid (average pH=3.3) and with low plant available phosphorous (average 9.3-10.1 mg kg^{-1}) (Gröngröft *et al.*, 2013).

The study area has a sub-humid summer rainfall climate with a pronounced wet season lasting from October to April. The mean annual precipitation is about 987 mm. Mean annual temperature is 20.4°C (Weber, 2013), with maximum temperatures above 40°C and minima below -7°C. Night frosts occur frequently in the valleys during the dry season, with highest frequency in June and July (Finckh *et al.*, 2016).

Apart from frost, dry season fire is the main disturbance factor for the open habitats in the area, occurring from May to September with a peak in July (Schneibel *et al*., 2013). These fires affect more than 70% of all geoxylic grasslands in the Okavango Basin annually, whereas for comparison only about 10% of the surface of dense miombo woodlands is affected (Stellmes *et al.*, 2013 b). Almost all fires in the study area are set by local people to clear grasslands for hunting and woodlands for agriculture (Schneibel *et al*., 2017).

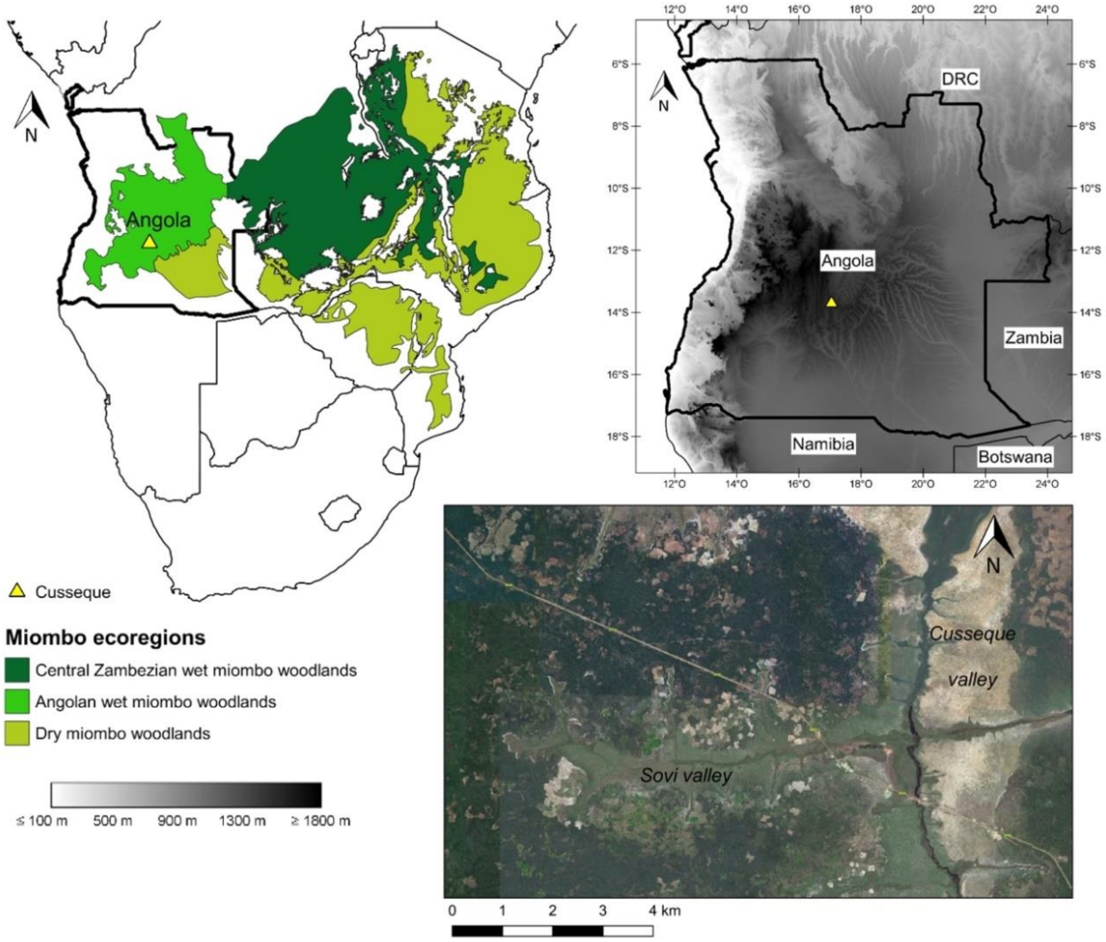

Figure 16: Location of the research site Chitembo. Left: the miombo ecoregions in Africa (based on Olson DM, Dinerstein E, 2002). Right: location in the upper Cubango catchment, Angola. The occurrence of open geoxylic grasslands on ferralitic soils (light green colour) and sandy deposits (white) is a characteristic feature in the valleys, contrasting with the woodlands on the hills (dark green).

Sample collection

We sampled 14 tree species from woodland habitats (9 Fabaceae and 5 non-Fabaceae) and 12 *geoxyle* species from open habitats (3 Fabaceae and 9 non-Fabaceae), all being very common in the area (Revermann *et al.*, 2017). An overview of the sampled species is given in Table S6. Samples were collected at the end of February and early March 2014 during the growing season and advanced wet season (Weber 2013; Revermann & Finckh 2013). At this time of the year the plants are fully developed. Five individuals from each tree and *geoxyle* species were sampled, whereby several sun exposed, fully expanded leaves that showed no symptoms of pathogen/herbivore attack were chosen.

Plant Functional Type (PFT) measurements

We selected plant functional traits known to show responses to a broad range of environmental factors. Links of the selected PFTs to ecophysiological mechanisms are well reported in the literature (Kattge *et al.*, 2011; Singh & Verma, 2020). For all species, we measured specific leaf area (SLA), leaf thickness (LT), leaf area (LA), leaf dry matter content (LDMC), wood density (WD), leaf nutrients content [carbon (LC), nitrogen (LN), phosphorus (LP), calcium (LCa), magnesium (LMg), potassium (LK)], C/N and N/P ratios and leaf water potential (LWP). Trait measurements were made following standardized protocols (Cornelissen *et al.*, 2003; Perez-Harguindeguy *et al.*, 2013; Muller, 2014).

SLA and LA: For each species, ten leaves were collected from each of the five individuals (totalling 50 leaves per species). Every leaf (excluding petioles) was scanned with a portable scanner to determine LA. Subsequently, the leaves were placed in a paper envelope and oven dried for 48 hours at 70°C until constant weight was achieved. Then we determined the leaf dry mass (LDM) using a high precision digital scale Kern 770. SLA was calculated dividing LA by LDM. LA for the scanned images was determined using XnViewMP software (available at: https://downloads.tomsguide.com/XnViewMP,0319-51391.html). For compound leaves we used only the leaflets, excluding petiole and/or rachis.

LT: Here, the same leaves were used as for the SLA determination. The measurements were made using a digital calliper at an intermediate position between the leaf margin and the midrib for each leaf. These individual measurements were then averaged to calculate species-mean values.

LDMC: Because water-saturated fresh leaf mass was not measured in the field, LDMC was estimated indirectly from equation as $\mathrm{LDMC} \approx 1/(\mathrm{SLA} \times \mathrm{LT})$ (Pérez-Harguindeguy *et al.*, 2013). Prior to calculations, values of LT were divided by 10 to achieve the same units as in SLA (cm).

WD: For geoxyles we collected woody samples (Diameter ≥ 2 cm) by digging up woody parts located belowground. For related tree species we collected branches of the same diameter. To measure wood density we used the volume displacement method (Osazuwa-Peters & Zanne, 2011). After drying the woody segment in an oven at 103 °C for at least 72 h, we measured the weight and calculated WD (ratio of the dry mass and the fresh volume). Values were averaged per species.

LN and LC: The same leave samples used for SLA and LT were analysed for all leaf nutrient contents. Dried samples were ground finely with a disc mill (from Retsch-solutions) and kept dry in an exsiccator. 100-200 mg of ground material was then used for analysis in the Elementar C/N Analyzer Vario Max Cube. Samples were burned at 900°C in presence of O_2 and the released NO_x gases were led through a column containing copper, zinc and tungsten, reducing them to N_2, which was quantified with a detector (Dumas Combustion Method) (Muller, 2014). The released CO_2 was quantified similarly. The measured carbon and nitrogen values were calculated into the C/N percentage of the respective samples, according to the calibration standards of known C/N content that were also combusted. The C/N ratio of each species was determined by dividing LC by LN.

LP, LCa, LMg and LK: About 250 mg of dry matter, finely ground, were digested with 8 ml of concentrated HNO_3 plus 800 µl H_2O_2 in a tightly closed Teflon tube in a microwave (1600 W) during 15 min of temperature ramp until 200°C and cooked for further 15 min at 200°C under pressure. The resulting product was diluted in 50 ml of distilled water. Before measurement with an inductively coupled plasma–optical emission spectrometer (ICP-OES, Spectro Arcos, Kleve, Germany), all samples were centrifuged to precipitate all particles. Before each run, a calibration was conducted with solutions of known concentration (0.0, 0.5, 1.0, 5.0, 10.0, 50.0 mg P/L) and a linear regression was fitted between P concentration and signal intensity.

To infer a robust estimate of total P concentration, five wavelengths (177.4 nm, 178.3 nm, 213.6 nm, 214.9 nm and 253.6 nm) were used, while concentrations of Ca/K/Mg were deduced from signals at 422.6 nm, 766.4 nm and 279.5 nm, respectively. Furthermore, the spectra were examined thoroughly to detect any interfering signals or background/underground disturbances, in which cases the errors were corrected and the concentrations recalculated. The concentrations inferred from signals of all element specific wavelengths were averaged.

Leaf Water Potential (LWP): The measurements were made under field conditions using a pressure Pump-Up Chamber Instrument (PMS Instrument Company USA; methodology (Scholander *et al*, 1965), a standard method used for plant water status measurements (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Measurements were made in the rainy (end of March) and dry seasons (early June) twice a day, at pre-dawn (5 hours) and midday (12 hours). All measurements were made within one hour after starting operation. Five leaves from five individuals per species (totalling 25 leaves) were successively cut and placed inside the chamber, with the cut end protruding from the seal. Once the chambers had been hermetically closed, pressure was gradually applied pumping the chamber. Once a water film appeared, pumping was stopped and the pressure indicated on the display was recorded. It was not possible to measure the leaf water potential of *Combretum platypetalum* in the dry season as it is leafless at this time of year. For this reason, we excluded the species when analysing LWP. Mean LWP was considered the mean of the two seasons (rainy and dry).

Data analysis

Comparisons of all plant functional traits within and between groups were calculated, using One-Way ANOVA (*t-test*). Principal components analysis (PCA) was used to analyse multivariate associations of the plant functional traits based on the scaled covariance matrix of variables. In particular, we investigated whether the spectra of trait-based plant strategies differed between life forms (tree / *geoxyle*) and symbiont type (Rhizobia yes / no; ECM yes / no).

Missing values for wood density in *Rhus exelliana* (due to the excessively soft-wood of the rhizome) and for leaf water potential in *C. platypetalum* (due to early leaf shedding) were imputed beforehand using imputePCA in R package missMDA (Josse & Husson, 2016). All statistical analyses were carried out using STATISTICA (Version 7) and packages FactoMineR (Husson *et al.*, 2010) and factoextra (Kassambara & Mundt, 2017) in R.

Results

Principal Component Analysis

The first six components of the PCA sufficiently explain the variance in the data (85.3 %), with the first two covering almost 50 % (Figure 17). The first component shows a strong positive correlation with SLA, LP and LN and a negative with C/N ratio. Tree species are separated from *geoxyle* species, as well as Fabaceae from non-Fabaceae and ECM species from non-ECM species. The second component correlates with LDMC, and reflects the well-known antagonism between LMg and LK. Geoxyles spread more across the first components than trees, indicating a higher variance across plant functional traits. WD and LA showed no clear pattern in this analysis.

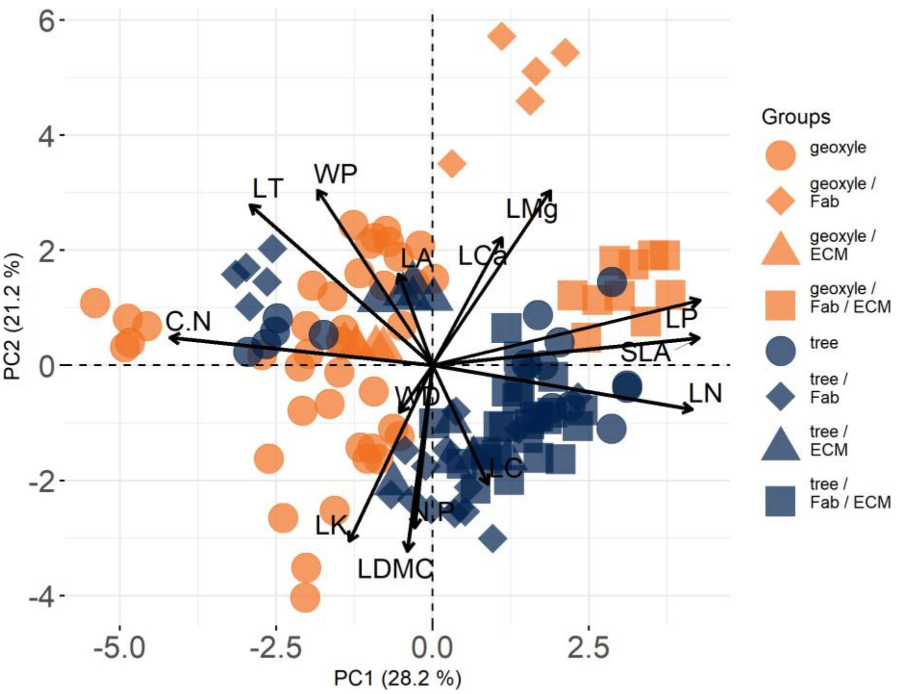

Figure 17: Principal component analysis (PCA) showing correlation of traits and species dispersion in relation to life form, belonging to Fabaceae and symbiotic status. The abbreviations are: SLA-Specific Leaf Area; LT- Leaf Thickness; LA- Leaf Area; LDMC- Leaf Dry Matter Content; WD- Wood Density; LN- Leaf Nitrogen; LC- Leaf Carbon; LP- Leaf Phosphorus; LMg- Leaf Magnesium; LCa- Leaf Calcium; LK- Leaf Potassium; C.N- Carbon to Nitrogen ratio; N.P- Nitrogen to Phosphorus ratio; WP- Water Potential. ECM- Ectomycorrhizal species, Fab- Fabaceae.

Within life form variation

We found highly significant differences for most plant functional traits within the life forms (Table 1). For geoxyles, all species differed significantly from each other in all plant functional traits, while for trees all but LMg differed between all species. The highest trait variance within life forms was found for WP, LT and C/N ratio (both), and LA plus LMg (geoxyles). For species specific details in the analysed traits, see Table S7 (geoxyles) and Table S8 (trees).

Table 8: Mean and standard error of all Plant Functional Traits, including results of One-Way ANOVA between geoxyles and trees and within each group. SLA- Specific leaf area; LT- Leaf thickness; LA- Leaf area; LDMC- Leaf dry matter content; WD- Wood density; LN- Leaf nitrogen content; LC- Leaf carbon content; LP- Leaf phosphorus content; LCa- Leaf calcium content; LMg- Leaf magnesium content; LK- Leaf potassium content; C/N- Carbon to nitrogen ratio; N/P- Nitrogen to phosphorus ratio; WP- Leaf water potential.

Traits	Mean±se		ANOVA between		ANOVA within			
	Geoxyles	Trees			Geoxyles		Trees	
			F	p	F	p	F	p
SLA (cm^2 g^{-1})	74.33±2.42	83.27±1.77	9.16	***	36.64	***	14.86	***
LT (mm)	0.35±0.01	0.28±0.01	27.48	**	143.40	***	89.51	***
LA (cm^2)	95.05±6.94	118.38±7.46	5.13	***	89.75	***	32.15	***
LDMC (mg g^{-1})	0.43±0.016	0.46±0.01	2.23	n.s.	19.05	***	12.67	***
WD (g cm^{-3})	0.62±0.02	0.56±0.01	13.68	***	3.13	***	12.01	***
LN (%)	1.51±0.06	1.97±0.07	26.04	***	35.60	***	35.44	***
LC (%)	49.57±0.35	51.03±0.47	6.0	**	8.88	***	15.58	***
LP (mg g^{-1})	0.94±0.05	1.12±0.04	8.45	***	27.53	***	23.70	***
LCa (mg g^{-1})	5.99±0.41	5.06±0.24	3.27	n.s.	25.33	***	7.10	***
LMg (mg g^{-1})	1.96±0.35	0.26±0.05	26.59	***	57.07	***	0.94	n.s.
LK (mg g^{-1})	7.48±0.47	10.21±0.09	38.02	***	56.30	***	15.58	***
C/N ratio	36.14±1.92	28.24±1.12	16.48	***	53.70	***	62.69	***
N/P ratio	17.05±0.65	18.08±0.5	1.60	n.s.	4.13	***	21.97	***
WP (bar)	-7.21±0.48	-9.29±0.5	8.66	***	366.15	***	245.34	***

(n.s.- not significant; **- significant; ***- highly significant, $p<0.05$).

Between groups variation

Comparison between trees and geoxyles

One-way ANOVA (Table 8) showed significant differences between geoxyles and trees for most plant functional traits, except for LDMC, LCa and N/P ratio. On average SLA, LA, LN, LC, LP, LK and WP were higher in trees than in geoxyles, while LT, WD, LMg and C/N ratio were higher in geoxyles than in trees.

Comparison between Fabaceae and non-Fabaceae

Separating Fabaceae species from non-Fabaceae species in both life forms, one-way ANOVA (Table S9) showed significant differences in many plant functional traits (Figure 18).

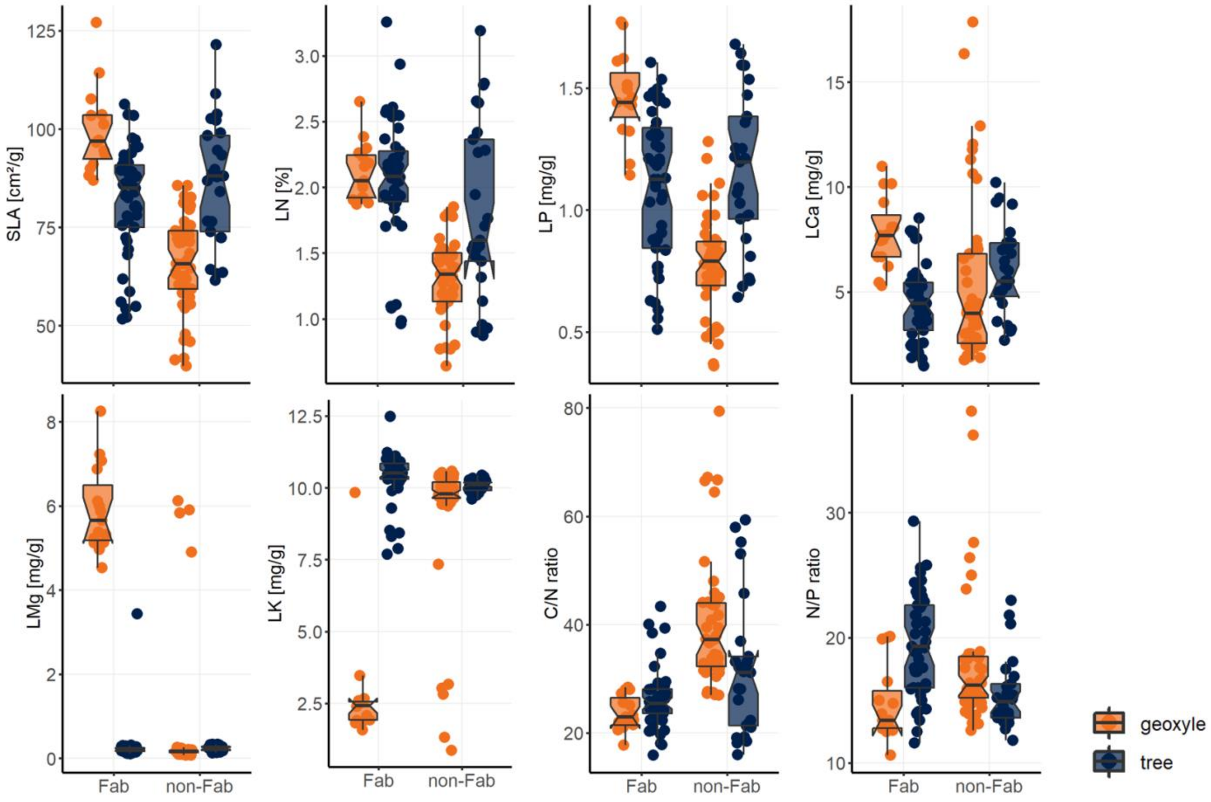

Figure 18: Plant functional traits (PFT) that differ significantly between geoxyles and trees with regard to lineage (Fabaceae (Fab) / non-Fabaceae (non-Fab)) (Table S9). Jittered points indicate variance of the data and non-overlapping notches show significant differences. Horizontal lines indicate the scale of values adopted for each PFT. Blue circles indicate trees and orange circles indicate geoxyles. SLA-Specific Leaf Area; LN- Leaf Nitrogen; LP- Leaf Phosphorus; LMg- Leaf Magnesium; LCa- Leaf Calcium; LK- Leaf Potassium; C.N- Carbon to Nitrogen ratio; N.P- Nitrogen to Phosphorus ratio.

Within geoxyles SLA, LN, LP, LCa and LMg were higher for Fabaceae species than for non-Fabaceae species, while LK, C/N and N/P ratios were higher for non-Fabaceae species. Within trees, SLA, LDMC, LN, LC, LP, LK and N/P ratio were higher for Fabaceae species than for non-Fabaceae species, while LT, LA, LCa and C/N ratio were higher for non-Fabaceae species.

Comparison between ECM associated and non-ECM associated species

To investigate the effect of ectomycorrhizal associations, we separated geoxyles and trees in ectomycorrhizal (ECM) species from species without this association (non-ECM) to analyse its influence in traits variation (Table S5). Regardless of the life form, again SLA and LP were significantly higher in ECM associated species. The differences in other traits varied between life forms, nevertheless, those traits that were significant relate to a better nutritional status of ECM associated species. Geoxyles differ in more traits between groups, reflecting the higher variance already encountered in the PCA (Figure 19).

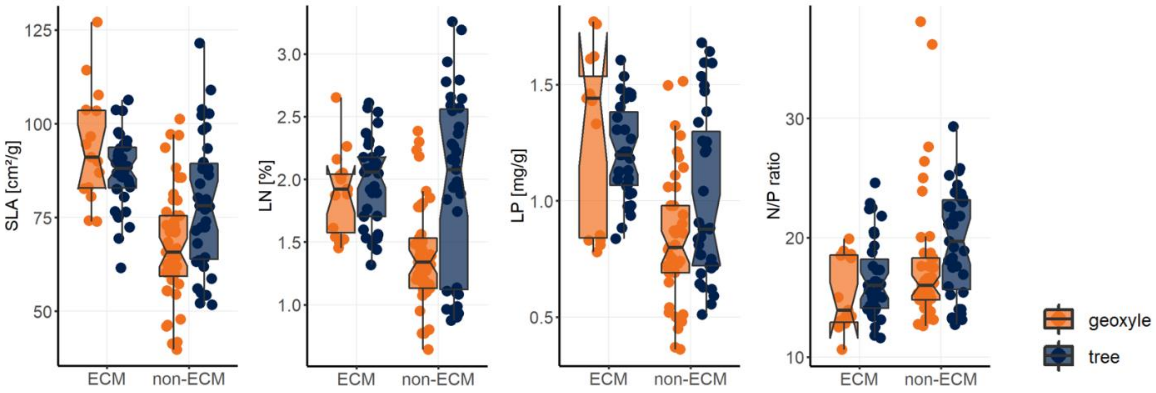

Figure 19: Plant functional traits (PFT) that differ significantly between geoxyles and trees with regard to symbiotic type (Ectomycorrhiza (ECM) / non-Ectomycorrhiza (non-EMC)) (Table S5). Jittered points indicate variance of the data and non-overlapping notches show significant differences. Horizontal lines indicate the scale of values adopted for each PFT. Blue circles indicate trees and orange circles indicate geoxyles. SLA-Specific Leaf Area; LN-Leaf Nitrogen; LP- Leaf Phosphorus; N.P- Nitrogen to Phosphorus ratio.

In a separate consideration, we looked for the influence of ectomycorrhiza within the dominant plant family of the miombo region. We compared how detarioid species and non-detarioid Fabaceae species (regardless of the life form) perform concerning the most important variables of the PCA (Figure 19, Table S5). Here, one-way ANOVA showed significantly higher LN and N/P ratio for non-detarioid species, while SLA and

LP were the opposite. There were no significant differences in C/N ratio between detarioid and non-detarioid species.

Table 9: One-way ANOVA comparing Detarioideae (Det) and non-Detarioideae (n-Det) legume species regarding Specific Leaf Area (SLA), Leaf Nitrogen (LN), Leaf Phosphorus (LP) contents, Carbon to Nitrogen (C/N) and Nitrogen to Phosphorus (N/P) ratios.

	Mean±stantard error		One-Way ANOVA	
	Det	n-Det	F	p
SLA (cm²/g)	92.93±1.92	85.63±2.75	34.10	***
LN (%)	2.12±0.04	2.35±0.09	7.43	***
LP (mg/g)	1.34±0.04	1.13±0.06	9.92	***
C/N ratio	24.66±0.52	22.75±0.86	3.99	n.s.
N/P ratio	15.65±0.57	21.11±0.77	34.10	***

Significant differences ($p<0.05$) are marked with asterisk. n.s. (no significant).

Discussion

What drives the functional differences between geoxyles and trees?

Apart from the large differences in height, the morphology of trees and geoxyles is strikingly similar. Reproductive traits do not show substantial differences while vegetative traits of geoxyles are restricted to a part of the phenetic space of trees (Meerts, 2017). However, until now the specific ecophysiological adaptations of these life forms have rarely been analysed. In this study, we show that they comprise distinct combinations of functional traits reflecting different ecophysiological strategies. We often observe trade-offs between two strategies, e.g. higher wood density (WD) of geoxyles which balances survival investment (high WD; Loehle, 1988; King *et al.*, 2006) against hydraulic conductivity (low WD; Borchert, 1994). Lower specific leaf area (SLA) and higher leaf thickness (LT) for geoxyles indicate that the lower xylem volume in *geoxyle* stems is associated to a lower volumetric flow rate of water. Two explanations spring to mind. Vinya *et al.* (2012) indicate coordination between branch hydraulic properties and leaf functional traits in miombo woodland trees. A lower leaf area ratio to sapwood area (huber value) in comparison to trees may simply result in reduced needs for high volumetric flow rates. However, we are not aware of any comparative study on huber values comparing trees with geoxyles. Alternatively, a relation of lower xylem vulnerability to cavitation, associated with higher WD (Barotto *et al.*, 2018), seems also plausible. This would be in line with the fact that the frost prone *geoxyle* habitats have also promoted strategies towards higher drought tolerance with increment on WD and mycorrhizal colonization (Midgley et al. 2010; Brunner et al. 2015; Volaire, 2018; Rodriguez-Zaccaro & Groover, 2019).

Another ecophysiological distinction is apparent in that geoxyles had higher magnesium (LMg) and lower potassium (LK) than trees and *vice versa*, representing the trade-off between investment in photosynthesis and adaptation to water stress (Hugouvieux *et al.*, 2002; Tůma *et al.*, 2004; Seyed *et al.*, 2012). Geoxyles optimize photosynthesis and relative growth rate. Since geoxyles are increasingly covered by tall C4-grasses from mid-December onward (Zigelski *et al.*, 2019), rapid growth with incipient vegetation period is beneficial. By allocating carbohydrates belowground to storage, geoxyles are able to cope with reduced assimilation in the later rainy season and during the dry season, and to resprout rapidly afterwards (Pausas *et al.*, 2018).

Strikingly, leaf dry matter content (LDMC) did not differ between life forms. Used as indicator of plants' resource use strategies, it represents a trade-off between rapid assimilation/growth (high LDMC) and efficient resource conservation (low LDMC) (Wilson *et al.*, 1999; Garnier *et al.*, 2001; Díaz *et al.*, 2004). Furthermore, LDMC is a reliable predictor of total aboveground net primary production (aNPP; Smart *et al.* 2017) and the similarity of LDMC between life forms suggests a comparable productivity of geoxylic grasslands and woodlands, but with different strategies of biomass allocation. "Underground forests" (White, 1976) are thus not only similar in terms of dominant genera (e.g. *Brachystegia, Cryptosepalum*), but also show similar productivity to aboveground forests.

Ecophysiological differentiations between geoxles and trees are thus driven by different stress and disturbance regimes in their respective environments. Nutrient limitation, however, affects all life forms in the miombo region regardless, as shown e.g. by the nitrogen and phosphorus content ratio (N/P) indicating consistently P-limited systems (Aerts & Chapin, 2000; Güsewell & Koerselman, 2002). In the following we discuss the role of symbiotic interactions to cope with this deficiency.

How are functional differences influenced by lineages with different symbiotic associations?

For several traits, we find lineage specific differences that show Fabaceae to have more favourable trait values. This is caused by their ability to fix nitrogen via microbial root symbionts, which directly affects important traits. SLA for example is strongly linked to growth rate and resource use by plants (Vendramini *et al.*, 2002) and is vital for resource capture, usage and availability (Grime *et al.*, 1997). Nitrogen is directly affecting vegetative growth and determining photosynthetic ability (Waite & Sack, 2010; Blonder *et al.*, 2011). Fabaceae are among the plants with highest LN and have in general low C/N ratios (McKey, 1994; Miller, 2000; Colgan *et al.*, 2015). This is in line with the negative correlation we found between C/N ratio and SLA, LN and LP. Besides, while environmental conditions are favourable, Fabaceae have a higher photosynthetic rate than most other plant families (Tuohy *et al.*, 1991; McKey, 1994). Often, they increase their competitive ability by allocating resources to storage organs (Pérez-Harguindeguy *et al.*, 2013). Furthermore, low C/N ratios in Fabaceae allow for high decomposition rates and, thus, for a quick nutrient turnover (Lewis *et al.*, 2016).

Why are Detarioideae so dominant in miombo ecosystems?

We compared several groups in our study, but we want to draw particular attention to the comparison between Detariodeae (ECM) and non-Detariodeae in the nutrient analyses (Tables 2, S4, S5). Leaf phosphorous content (LP) was significantly higher in trees than in geoxyles, in Fabaceae than in non-Fabaceae and in ECM than in non-ECM species. Phosphorus is essential for plant growth and reproduction (White & Hammond, 2008), but limited in the soils of the study area (Gröngröft *et al.*, 2013, own measurements). Besides ECM, plants adapt to low phosphorous availability through conservative use in tissues, e.g. redeployment (Hedin 2004; McGroddy *et al.* 2004; Güsewell, 2005; Minden & Kleyer, 2014) and changes in biomass allocation (Hermans *et al.* 2006) within the organism during ontogeny.

The dominant genera of the miombo are detarioid with ECM (Högberg, 1982). They are thereby enabled to take up P directly from organic matter (Högberg & Nylund 1981; Högberg & Piearce 1986; Frost, 1996; Hall *et al.*, 2019) and to stimulate biological N-fixation (Tiessen, 2008). Contrariwise, non-detarioid legumes have to invest fixed nitrogen into phosphatase production to cope with phosphorous-limitation (Houlton *et al.*, 2008).

Lower LP in geoxyles compared to trees may partly be biased by the lower proportion of detarioid geoxyles (25% of species) compared to trees (64%) in our analysis. Yet, we also find lower LP in geoxyles compared to trees among non-Fabaceae, indicating that this pattern also reflects less soil organic matter in geoxylic grasslands due to their much higher fire frequency compared to woodlands (Stellmes et al., 2013 b).

Conclusions

Our study found significant differences between geoxyles and trees co-occurring in contiguous areas of the Angolan Central plateau for almost all analyzed traits. These differences reflect adaptations to the disturbance regime and environmental stresses of their respective habitats. Each group developed a wide range of responses to cope with these local environmental conditions, particularly through changes in biomass allocation (below or aboveground), ecophysiological strategy and leaf/wood morphology.

Lineage specific symbiotic interactions like ECM or rhizobia, which are improving nutrient uptake, dominate the pattern of variation in most traits. Strikingly, key traits like specific leaf area, nitrogen and phosphorus content were dominated by detarioid Fabaceae. ECM associations provide even better nutrient provision than rhizobia for both tree and *geoxyle* species. The striking dominance of detarioid species in both grasslands and woodlands of the miombo is linked to their symbionts, which provide advantageous ecophysiological adaptations to nutrient deficient soils and environmental stresses. With our study, we provide new insights into little-studied, fundamental aspects of biogeochemical cycles in the miombo region.

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Author contribution

The research was firstly conceived by ALG and MPMA and subsequently performed by all co-authors. Field work was carried out by ALG together with FMPG, MPMA, RR and MF. Laboratory analysis was carried out by PM. FL assured logistical and bureaucratic support for the research. Data analysis and interpretation of results were performed by ALG, RR, MF, MPMAA and PM. The writing of the manuscript was done by ALG, PM and MF with contribution of all co-authors.

CHAPTER 6- Synthesis

Geoxyle co-dominated ecosystems

In this overview chapter, I shortly review the current knowledge on distribution and diversity of geoxyles and geoxyle grasslands in Angola, their ecology and their evolutionary history and I point at important knowledge gaps.

Geoxyle grasslands, which form at landscape scale a mosaic with miombo woodlands, constitute one of the most particular ecosystem types of Angola. Early on, they attracted the attention of vegetation scientists, as shown by Gossweiler & Mendonça’s (1939) classification as Ericilignosa, followed by Barbosa’s (1970) typification as “Anharas de Ongote” and “Chanas da Borracha”. White (1976) was the first author who gave a general overview on geoxyles and geoxyle grasslands in the Zambezian phytochorion, with a special focus on the areas covered by Kalahari sands.

Our results show, that from about 198 geoxyles known from the Zambezian phytochorion at least 121 species occur in Angola and about 10% of those are Angolan endemics. However, large areas with extended geoxyle grasslands in eastern Angola are still little explored, so these data have to be seen as preliminary.

Frost and/ or fire are important environmental drivers in geoxyle habitats, while seasonal flooding and waterlogging seem to impede the growth of most geoxyle species. In seasonally flooded landscapes like the flat plains of the Cameia National Park in eastern Angola the geoxyles occupy mostly highlying microsites like fossil dunes and termite mounds, thus avoiding prolonged waterlogging.

Important knowledge gaps concern ecosystem services related to geoxyle dominated ecosystems, but also the astonishing convergent evolution of so many geoxyles from different plant families in the Zambezian phytochorion is far from being understood. The role environmental drivers played for this process is still in discussion. I only gathered first insights on the functional benefits the geoxylic habitat brought along for surviving in these disturbance prone habitats.

The lack of floristic data and the just mentioned research gaps indicate once more the need of further research on distribution, biodiversity, ecology and conservation needs to improve our scientific knowledge about this singular ecosystem. Aspects of ecosystem services delivered by geoxyle grasslands and aspects of the functional benefits of the geoxyle life form have been addressed in the following chapters of my thesis.

Geoxyle grasslands in south-central Angola: vegetation dynamics, root structure, belowground biomass and soil characteristics

The following Chapter 3 dealt with woody belowground biomass and related carbon stocks, soil properties of and human impact on vegetation types shaped by geoxyle species on the Angolan Central Plateau. This is the first study to measure woody belowground biomass in geoxyle dominated Afrotropical grasslands, the so called "underground forests of Africa". It significantly advances our understanding of carbon storage in ancient tropical grasslands, showing that the belowground biomass of *Brachystegia russelliae* dominated geoxyle grasslands reaches 44 t/ha and almost equals the amount of above ground biomass of neighbouring miombo woodlands. Almost the entire woody below-ground biomass is located in the top 30 cm of the soil. Thus, this chapter emphasizes the high relevance of below-ground biomass in geoxyle grasslands for carbon stock accountingof African dry-tropical ecosystems.

Both major vegetation types, *B. russelliae* dominated geoxyle grasslands on ferralitic soils and *Parinari capensis* dominated geoxyle grasslands on arenosols were extremely acid and showed a low nutrient availability. However, both grassland types differed strongly in EVI and fire-seasonality. *Brachystegia russelliae*-grasslands showed a considerably higher EVI than *Parinari capensis*-grasslands all year round. The latter burnt almost twice as frequently as *Brachystegia russelliae*-grasslands in a ten year period. Man-made disturbances and differences in fire-resilience between the two vegetation types seem to control the respective disturbance regimes.

Tree or not a tree: differences in plant functional traits among geoxyles and closely related tree species

Chapter 4 addresses functional traits of geoxyles, comparing them with closely related, congeneric or conspecific trees. I selected six species pairs that are common in the study area, i.e. *Brachystegia russelliae* vs. *Brachystegia longifolia* (Fabaceae-Detarioideae); *Cryptosepalum exfoliatum* subsp. *suffruticans* vs. *Cryptosepalum exfoliatum* subsp. *pseudotaxus* (Fabaceae-Detarioideae); *Combretum platypetalum* vs. *Combretum zeyheri* (Combretaceae); *Parinari capensis* vs. *Parinari curatellifolia* (Chrysobalanaceae); *Syzygium guineense* subsp. *macrocarpum* (suffrutex form vs. tree form) (Myrtaceae); *Uapaca nitida* var *suffrutescens*/ *Uapaca nitida* var. *nitida* (Phyllanthaceae). I measured plant functional traits known to show responses to a broad range of environmental factors aiming to find adaptive traits of geoxyles and trees to their respective environments. I specifically selected traits linked to known eco-physiological mechanisms like specific leaf area, leaf thickness, leaf area, leaf dry matter content, wood density, several leaf nutrient concentrations, C:N and N:P ratios and leaf water potential.

Results did not show a trait dualism between trees and geoxyles. The growth form transition seems to be largely decoupled from leaf economics. Taxon related responses to specific environmental stresses and habitat conditions in a multdimensional trait space dominate the detected differences among the species pairs.

Functional traits and symbiotic associations of geoxyles and trees explain the dominance of detarioid legumes in miombo ecosystems

Chapter 5 addresses the question, in how far these taxon specific responses in traits of geoxyles and trees are based on phylogenetically inherited symbiotic interactions, with a special view on the role of ectomycorrhizal associations. To do so, I measured and compared the same plant functional traits as before for a larger set of geoxyle and tree species (12 and 14, respectively) which all co-occur in the Cusseque area.

As typical for the miombo ecoregion, the study area is covered by a mosaic of woodlands and geoxyle grasslands, both dominated by detarioid legume species.

This dominance of Detarioidae is remarkable but so far little understood. I therefore compared the plant functional traits (PFTs) according to life form (trees, geoxyles), lineage (e.g. Fabaceae, non Fabaceae; Detarioideae, non-Detarioideae) and symbiont association (ectomycorrhiza, rhizobia), aiming to better understand if plant functional traits reflect group-specific adaptations to their respective environmental conditions.

Results showed both lineage specific adaptations to nutrient poor soils and life form specific strategies to cope with environmental stresses. Higher wood density and leaf thickness can be regarded as a response to harsher conditions in open grassland environments. Fabaceae as a whole and ectomycorrhizal species showed higher leaf nutrient contents. The specific symbiotic associations of Detarioidae clearly have specific advantages to capture phosphorous in comparison to non-Fabaceae and Rhizobia associated Fabaceae, as shown e.g. by their significantly higher phosphorous content. Thus, the hyperdominance of detarioid species in miombo ecosystems is linked to their ectomycorrhizal association. This finding provides new insights into fundamental aspects of biogeochemical cycles in the miombo ecosystems.

Final remarks

Based on local studies on the Angolan plateau, the presented study has contributed to a broader understanding not only of geoxyle grasslands but also to environmental constraints of the miombo woodlands on the Bié plateau and beyond. The study provides for the first time data for belowground woody biomass and associated carbon storage of Zambezian geoxyle grasslands, indicating dimensions which are relevant for subcontinental carbon balances. Together with my co-authors, I have measured and compared PFT that allowed me to better understand the ecophysiological adaptations of geoxyles to harsh and disturbance prone environmental conditions on the Angolan plateau. Finally I showed the role of microbiological associations for the dominance of Detarioid species in grasslands and woodlands on the Angolan plateau and probably the wider miombo ecoregion. One of the fundamental vegetation patterns of the African continent, the divide between dominant Rhizobia associated legume trees in the dry savannas and dominant ectomycorrhiza associated Detarioidae in the wet savannas and dry tropical forests seem to be (at least partly) based on different strategies of nutrient capture.

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① Brachyst
0,185
② Brachyst
0,1243 lb
4/3/14
⑤
⑦ Brach
Syg
Uap 3/3/14
0,055 lb
④ Uap 4/3/14
0,097 lb
Uap 4/3/14
0,044 lb
① Syg 3/3/14
0,093 lb
③ 0,082 lb
② Syg 4/3/14
0,090 lb

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Author contributions

Chapter 1: This chapter was written fully by myself and adapted from the initial project proposal, presented for a doctoral degree at the Department of Biology, Institute of Plant Science and Microbiology of the University of Hamburg.

Chapter 2: This chapter was conceived and written jointly by PZ, AG and MF looking at the past and recent exploration of the geoxyle flora and vegetation of Angola. The manuscript reviews historic steps of the exploration of Angola's geoxyle flora and recent research results. This chapter is part of the book "Biodiversity of Angola, Science & Conservation: A modern synthesis published recently by Springer.

Chapter 3: The research was conceived by AG, and supervised by MA and MF. All authors contributed to field work for this paper, except FL who assured logistical and bureaucratic support for the research. AG drafted the manuscript and performed the statistical analyses supervised by RR and MF. RR provided the map of the study area. All co-authors contributed to the draft of the manuscript and the revision process.

Chapter 4: Data for this paper were gathered during field work in the Cusseque area by AG, supported by FG and MA. Methods and scope of the paper were developed jointly among all co-authors. AG drafted the manuscript and did the data analyses. RR, MF and Norbert Juergens contributed additional analyses and comments improving the paper. FL assured logistical and bureaucratic support for the research.

Chapter 5: The research was designed by AG with supervision of MA. Field work was carried out by AG together with FG, MA, RR and MF. Laboratory analyses were carried out by PM. FL assured logistical and bureaucratic support for the research. Data analyses and interpretation of results were done by AG with cooperation by PM, RR, MA and MF. The manuscript was drafted by AG with contributions by PM and MF. All co-authors commented on the final draft.

Chapter 6: This chapter was entirely written by AG synthetising the most important findings comprised by the thesis. In these papers I had significant contributions in the interpretation of the results and in the writing of manuscripts parts.

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Dedication

This work is dedicated to my parents, Jacinto Gomes and Emília Luís Bambi, to my wife Ruth da Conceição Job Cahengue Gomes, to our children Cremilda, Ester, Edgar, Rusândio and Tuwizana for their unconditional love, support and patience during the long periods of my absence, sometimes without any communication.

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SUPPORTING INFORMATION

Table S1: Plots location with biomass in g/0.25 m^2, inferred in ton/ha. Vegetation type: bg- *Brachystegia* grassland; pg- *Parinari* grassland.

#	**Latitude**	**Longitude**	**Altitude**	**vegetation type**	**Biomass**	
					g/0.25m^2	**ton/ha**
27001	13.70305°	17.06560°	1540	bg	1430	57.2
27002	13.70375°	17.06529°	1471	bg	1000	40
27003	13.68027°	16.99178°	1442	bg	2030	81.2
27004	13.67840°	16.98407°	1547	bg	1350	54
27007	13.70657°	17.06010°	1540	bg	2380	95.2
27008	13.65637°	17.01741°	1515	bg	560	22.4
27009	13.66040°	17.01403°	1562	bg	980	39.2
27012	13.69826°	17.08528°	1451	bg	970	38.8
27013	13.68868°	17.08887°	1522	bg	1470	58.8
27014	13.70506°	17.06548°	1397	bg	1440	57.6
27015	13.70769°	17.06585°	1543	bg	1250	50
27016	13.69880°	17.04457°	1486	bg	1890	75.6
27017	13.70598°	17.04267°	1554	bg	1230	49.2
27018	13.70266°	17.07129°	1470	bg	1120	44.8
HP01	13.70314°	17.07074°	1530	bg	417	16.68
HP02	13.70254°	17.06912°	1543	bg	1237	49.48
HP03	13.70397°	17.06878°	1534	bg	1127	45.08
HP04	13.70250°	17.06835°	1553	bg	114	4.56
HP05	13.70433°	17.06794°	1524	bg	641	25.64
HP06	13.70349°	17.06727°	1527	bg	682	27.28
HP07	13.70385°	17.06729°	1522	bg	797	31.88
HP08	13.70307°	17.06696°	1522	bg	1909	76.36
HP09	13.70289°	17.06611°	1515	bg	910	36.4
HP10	13.70286°	17.06552°	1527	bg	1066	42.64
HP11	13.70328°	17.06468°	1523	bg	1580	63.2
HP12	13.70342°	17.06387°	1525	bg	1189	47.56
HP13	13.70263°	17.06360°	1530	bg	408	16.32
HP14	13.70175	17.06374°	1549	bg	428	17.12
HP15	13.70129	17.06279°	1542	bg	476	19.04
27005	13.72252º	17.09781º	1472	Pg	800	32
27006	13.69849º	17.10631º	1475	Pg	520	20.8
27010	13.73372º	17.09409º	1446	Pg	920	36.8
27011	13.71732º	17.09150º	1512	pg	1140	45.6
23601	13.70858º	17.10485°	-	pg	378	15.12
23602	13.70728º	17.10361°	-	pg	424	16.96
23603	13.70789º	17.10324°	-	pg	693	27.72
23604	13.70786º	17.10229°	-	pg	37	1.48
23605	13.70790º	17.10029°	-	pg	38	1.52
23606	13.70825º	17.09911°	-	pg	136	5.44
23607	13.70813º	17.09585°	-	pg	14	0.56
23608	13.70749º	17.09497°	-	pg	176	7.04

23609	13.70552º	17.09408°	-	pg	228	9.12
23610	13.70555º	17.09327°	-	pg	64	2.56
23611	13.70531º	17.09326°	-	pg	61	2.44
23612	13.70721º	17.09258°	-	pg	532	21.28
23613	13.70839º	17.09202°	-	pg	541	21.64
23614	13.70780º	17.09175°	-	pg	511	20.44
23615	13.70701º	17.09003°	-	pg	679	27.16

Table S2: Univariate statistics of BGB in two types of geoxylic grasslands.

	BGB (ton/ha)	
	Par. Grass.	Brach. Grass.
Mean	16.6	44.25
Std. error	3.05	3.99
Variance	177	463
Stand. dev	13.3	21.5
Coeff. var	80.1	48.6

Table S3: Soil characteristics of the *Brachystegia* grassland.

#	Depth (cm)	Particle size analysis (%)			pH			Exchangeable bases (Cmole.dm^{-3})				P (mg.dm^{-3})	Al (mg.dm^{-3})	Al + H (mg.dm^{-3})	CTC (pH 7)	Sum of bases (Cmole.dm^{-3})	V (%)	m(%)
		clay	silt	sand	H_2O	KCl	Ca_2Cl	K	Na	Ca	Mg							
27001	0-10	9.50	5.50	85.00	5.13	4.30	4.39	16.15	0.00	0.84	4.54	3.52	0.30	4.60	26.42	21.52	81.45	18.55
	10-30	33.25	9.25	57.50	4.96	4.18	4.02	13.29	0.00	0.61	5.66	4.39	0.70	4.30	24.55	19.55	79.63	20.37
	30-50	32.00	13.00	55.00	4.78	4.36	4.14	11.38	0.00	0.62	7.41	4.66	0.50	4.00	23.92	19.42	81.19	18.81
27002	0-10	7.85	7.15	85.00	5.41	5.32	5.03	14.24	0.00	2.74	16.65	6.62	0.20	4.50	38.33	33.63	87.74	12.26
	10-30	3.25	6.75	90.00	4.92	4.50	4.55	10.43	0.00	0.68	0.00	3.39	0.30	4.30	15.71	11.11	70.72	29.28
	30-50	0.00	2.50	97.50	4.96	4.34	4.28	15.19	0.00	0.79	0.00	3.75	0.50	4.00	20.48	15.98	78.03	21.97
27003	0-10	18.50	9.00	72.50	5.10	4.48	4.47	8.53	0.00	1.03	0.00	5.66	0.50	4.40	14.45	9.55	66.09	33.91
	10-30	3.00	7.00	90.00	4.27	4.21	4.07	2.81	0.00	1.37	0.00	20.62	0.50	4.00	8.68	4.18	48.16	51.84
	30-50	12.50	7.50	80.00	4.12	4.16	4.00	1.86	0.00	1.55	0.00	8.52	0.50	3.90	7.81	3.41	43.66	56.34
27004	0-10	0.00	2.50	97.50	5.00	4.45	4.43	7.58	0.00	1.43	2.86	5.16	0.40	4.30	16.56	11.86	71.62	28.38
	10-30	2.50	2.50	95.00	4.15	4.20	4.04	3.77	0.00	1.65	3.03	3.93	0.60	4.20	13.25	8.45	63.77	36.23
	30-50	11.00	4.00	85.00	4.32	4.20	4.02	4.72	0.00	1.68	4.47	3.52	0.90	4.10	15.86	10.86	68.47	31.53
27007	0-10	0.25	6.00	93.75	5.33	5.11	4.82	10.43	0.00	3.46	11.26	4.34	0.30	3.70	29.15	25.15	86.28	13.72
	10-30	0.00	10.00	90.00	4.29	4.20	4.15	7.58	0.00	0.97	0.81	2.57	0.50	3.50	13.36	9.36	70.06	29.94
	30-50	10.85	9.15	80.00	4.08	4.06	3.93	12.34	0.00	1.39	1.99	3.62	1.40	4.10	21.21	15.71	74.07	25.93
27008	0-10	0.00	0.00	100.00	4.41	3.76	3.91	1.86	0.00	0.00	4.05	3.07	0.50	4.20	10.61	5.91	55.70	44.30
	10-30	3.20	4.00	50.30	4.37	4.16	4.02	1.86	0.00	0.00	4.99	3.43	0.40	3.70	10.95	6.85	62.56	37.44
	30-50	6.00	9.20	50.00	4.54	4.49	4.30	0.91	0.00	0.00	6.72	4.57	0.50	3.60	11.73	7.63	65.05	34.95
27009	0-10	2.00	7.20	60.00	4.99	4.47	4.48	4.72	0.00	1.53	3.08	4.12	0.40	4.20	13.93	9.33	66.98	33.02
	10-30	1.25	2.50	96.25	4.51	4.38	4.24	1.82	0.00	0.00	0.00	6.80	0.50	3.50	5.82	1.82	31.27	68.73
	30-50	0.40	5.85	93.75	4.34	3.34	4.20	1.82	0.00	8.32	0.00	3.89	0.40	3.60	14.14	10.14	71.71	28.29
27012	0-10	0.00	8.20	83.20	4.91	4.29	4.28	7.33	0.00	25.34	0.00	5.52	0.50	1.00	34.17	32.67	95.61	4.39
	10-30	10.85	9.40	84.50	4.45	4.23	4.11	2.74	0.00	35.94	0.00	9.84	0.60	0.20	39.48	38.68	97.97	2.03
	30-50	3.20	6.15	85.30	4.28	4.14	4.00	2.74	0.00	48.31	0.00	7.80	0.90	0.20	52.15	51.05	97.89	2.11

	0-10	1.25	6.00	86.20	5.27	4.72	4.69	14.67	0.00	0.00	0.00	4.62	0.30	0.60	15.57	14.67	94.22	5.78
27013	10-30	0.40	4.00	87.25	5.09	4.37	4.40	9.16	0.00	7.10	0.00	6.02	0.40	0.40	17.06	16.26	95.31	4.69
	30-50	0.30	2.00	88.50	4.96	4.20	4.14	22.01	0.00	20.14	0.00	7.34	1.30	0.60	44.05	42.15	95.69	4.31
	0-10	0.50	0.00	89.40	4.59	3.98	4.07	7.33	0.00	29.04	0.00	4.52	0.50	1.00	37.87	36.37	96.04	3.96
27014	10-30	0.25	6.00	93.75	4.31	4.13	4.03	2.74	0.00	40.49	0.00	9.34	0.90	0.80	44.93	43.23	96.22	3.78
	30-50	3.50	6.50	90.00	4.14	4.12	4.05	1.82	0.00	0.00	0.00	8.89	0.60	0.60	3.02	1.82	60.26	39.74
	0-10	0.00	3.75	96.25	4.93	4.41	4.44	6.41	0.00	11.94	0.00	6.02	0.50	0.20	19.05	18.35	96.33	3.67
27015	10-30	3.50	6.50	90.00	4.84	4.14	4.09	5.49	0.00	19.43	0.00	8.16	0.60	0.20	25.72	24.92	96.89	3.11
	30-50	3.00	14.50	82.50	4.52	4.09	3.98	7.33	0.00	28.66	0.00	5.80	1.00	0.60	37.59	35.99	95.74	4.26
	0-10	0.00	2.50	97.50	4.91	4.35	4.38	3.77	0.00	0.00	0.57	5.80	0.30	0.20	4.83	4.33	89.65	10.35
27016	10-30	4.25	5.75	90.00	4.93	4.26	4.09	1.86	0.00	0.00	0.69	5.80	0.30	1.60	4.45	2.55	57.30	42.70
	30-50	7.80	2.20	90.00	4.56	4.26	4.08	1.86	0.00	0.00	0.80	6.89	0.60	0.20	3.46	2.66	76.88	23.12
	0-10	4.50	8.00	87.50	4.81	4.74	4.76	1.86	0.00	0.00	1.18	4.66	0.30	0.80	4.14	3.04	73.43	26.57
27017	10-30	5.25	7.25	87.50	5.40	4.48	4.68	5.67	0.00	0.00	0.00	4.66	0.20	0.60	6.47	5.67	87.64	12.36
	30-50	4.88	7.63	87.50	5.11	4.61	4.72	3.77	0.00	0.00	0.59	4.66	0.25	0.70	5.31	4.36	82.11	17.89
	0-10	5.25	9.75	85.00	5.57	4.75	4.78	10.43	0.00	0.00	0.00	4.66	0.20	1.20	11.83	10.43	88.17	11.83
27018	10-30	7.63	8.63	83.75	5.28	4.45	4.46	5.53	0.00	0.01	0.00	5.05	0.40	0.90	9.83	8.53	86.78	13.22
	30-50	10.00	7.50	82.50	4.98	4.14	4.14	0.62	0.00	0.01	0.00	5.43	0.60	0.60	7.83	6.63	84.67	15.33

Table S4: Soil characteristics of the *Parinari* grassland.

#	Depth (cm)	Particle size analysis (%)			pH			Exchangeable bases (Cmole.dm^{-3})				P (mg.dm^{-3})	Al (mg.dm^{-3})	Al + H (mg.dm^{-3})	CTC (pH 7)	Sum of bases (Cmole.dm^{-3})	V (%)	m(%)
		clay	silt	sand	H_2O	KCl	Ca_2Cl	K	Na	Ca	Mg							
2149	0-10	3.8	1.9	94.3	4.9	3.8	3.9	1.48	0.68	0.18	0	1.39	0.60	0.6	2.94	2.34	3.8	1.9
	10-30	3.45	2.175	94.38	5.10	4.2	4.15	4.91	0.93	0.07	0	1.41	0.44	0.4	6.31	5.91	3.45	2.175
	30-50	7.9	3.35	88.75	5.4	4.4	4.2	0.11	4.68	0.49	0	1.34	0.50	0.5	5.78	5.28	7.9	3.35
2151	0-10	4.2	2.05	93.75	4.8	4	3.9	0.11	0.68	0	0	1.25	0.7	0.7	1.49	0.79	4.2	2.05
	10-30	8	5.25	86.75	4.9	4.3	4.05	0.46	0.68	0.12	0	1.80	0.72	0.7	1.96	1.26	8	5.25
	30-50	12.5	6.875	80.63	5.07	4.25	4.05	0.80	0.43	0.26	0	1.55	1.09	0.85	2.33	1.48	12.5	6.875
2153	0-10	0	2.5	97.5	4.9	3.66	3.8	0.8	0.68	0.38	0	1.30	0.50	0.5	2.36	1.86	0	2.5
	10-30	3.4	0	96.6	5.15	4.18	4.2	0.11	0.18	0.23	0	1.34	0.36	0.35	0.87	0.52	3.4	0
	30-50	2.5	1.25	96.25	5.15	4.41	4.35	1.83	0.94	0.09	0	1.80	0.63	0.5	3.35	2.85	2.5	1.25
2165	0-10	2.9	3.35	93.75	4.91	3.75	3.9	5.59	0.68	0.14	0		0.20	0.2	6.60	6.40	2.9	3.35
	10-30	2.6	1.15	96.25	5.22	4.32	4.2	1.14	0.68	0.05	0	0.39	0.41	0.4	2.27	1.87	2.6	1.15
	30-50	2.2	5.4375	92.38	5.36	4.46	4.25	3.88	0.68	0.14	0	1.75	0.35	0.35	5.04	4.69	2.2	5.4375
23315	0-10	0.0	8.3	91.8	5.8	4.9	4.9	0.03	0.54	1.89	0.00	0.570	0.30	0.3	2.76	2.46	0.0	8.3
	10-30																	
	30-50	0.1	7.4	92.5	5.0	3.9	4.0	0.03	0.22	1.36	0.00	0.615	0.1	0.1	1.71	1.61	0.1	7.4
23618	0-10	0	15	85	4.81	3.97		0.31	1.08	0.13	0.61	0.71	0.0				0	15
	10-30																	
	30-50	3.3	9.2	87.5	5.02	4.3	4.17	0.28	1.18	0.11	0.28	1.02	0.00	0.4	1.07	0.67	3.3	9.2
23619	0-10	0	5	95	4.76	4.07	3.96	0	0	0.00	0	0.89	0.50	0.5	0.50	0.00	0	5
	10-30																	
	30-50	0	2.5	97.5	4.86	4.43	4.23	0	0	0.00	0	0.71	0.40	0.4	0.40	0.00	0	2.5
27005	0-10	0.00	0.00	100.00	4.38	4.01	3.97	2.81	0.00	1.98	5.71	3.48	0.50	4.50	15.50	10.50	0.00	0.00
	10-30	0.00	0.00	100.00	3.98	4.21	4.09	0.91	0.00	2.62	7.61	3.43	0.40	3.90	15.44	11.14	0.00	0.00
	30-50	0.00	2.50	97.50	3.89	4.33	4.09	0.91	0.00	0.97	1.78	4.21	0.50	3.40	7.56	3.66	0.00	2.50

	0-10	0.00	2.50	97.50	4.07	3.85	3.77	4.72	0.00	1.07	3.40	5.21	0.60	4.50	14.29	9.19	0.00	2.50
27006	10-30	0.00	3.75	96.25	4.26	4.20	4.04	1.86	0.00	1.50	4.64	6.21	0.60	4.20	12.81	8.01	0.00	3.75
	30-50	0.00	2.50	97.50	4.49	4.30	4.14	0.91	0.00	1.90	6.52	4.34	0.60	3.90	13.82	9.32	0.00	2.50
	0-10	0.50	12.00	87.50	4.89	4.35	4.38	10.08	0.00	17.33	0.00	3.21	0.70	1.80	29.91	27.41	0.50	12.00
27010	10-30	11.00	6.50	82.50	4.40	4.22	4.04	5.49	0.00	0.00	0.00	5.34	0.60	1.20	7.29	5.49	11.00	6.50
	30-50																	
	0-10	0.00	3.75	96.25	4.73	3.99	4.06	10.08	0.00	0.00	0.00	3.75	1.00	1.40	12.48	10.08	0.00	3.75
27011	10-30	8.50	11.50	80.00	4.67	4.21	4.05	6.41	0.00	4.39	0.00	5.16	1.20	2.20	14.20	10.80	8.50	11.50
	30-50	8.20	9.30	82.10	4.80	4.19	4.06	6.41	0.00	15.58	0.00	3.52	0.10	1.00	23.09	21.99	8.20	9.30

Table S5: One-way ANOVA comparing Detarioideae (Det) and non-Detarioideae (n-Det) species regarding SLA, LN, LP, C:N and N:P, traits determining plant nutritional status.

	Mean±stantard error		**One-Way ANOVA**	
	Det	n-Det	F	P
SLA (cm²/g)	92.93±1.92	85.63±2.75	34.1	***
LN (%)	2.12±0.040	2.35±0.085	7.43	***
LP (mg/g)	1.34±0.037	1.13±0.059	9.92	***
C:N ratio	24.66±0.52	22.75±0.86	3.99	n.s.
N:P ratio	15.65±0.57	21.11±0.77	34.1	***

Significant differences are marked with asterisc.

Table S6: Characterization of species pair (geoxylic versus trees) closely related used to compare Plant Functional Traits in the chapter 2 of this thesis.

Family	**Species**	**Life form**	**habitat**	**leaves**	**Height (m)**	**Leaf phenology**		**Vouchers**
						flush	**fall**	
Myrtaceae	*Syzygium guineense* (Willd.) DC. subsp. *macrocarpum* (Engl.) F.White (1)	geoxyle	geoxylic grasslands on ferrallitic soils	laurophyllous, single, elliptic, lanceolate or ovate-elliptic	1	evergreen	evergreen	HBG 135802 HBG 143204
	Syzygium guineense (Willd.) DC. subsp. *macrocarpum* (Engl.) F.White (1)	Small multi-stemmed tree	open forest and forest edges at top-slopes on ferrallitic soils	laurophyllous, single, elliptic, lanceolate or ovate-elliptic	5-6	evergreen	evergreen	HBG 135805
Chrysobalanaceae	*Parinari capensis* Harv.	geoxyle	geoxylic grasslands on sandy soils	sclerophyllous, single, oblanceolate to oblong or oblong-elliptic	0.05	evergreen	evergreen	HBG 132664
	Parinari curatellifolia Planch. ex Benth.	tree	forest edges between top- and mid-slopes mostly on ferrallitic soils	sclerophyllous, single, oblong	15 or more	evergreen	evergreen	HBG 132671
Combretaceae	*Combretum platypetalum* Welw.	geoxyle	geoxylic grasslands and disturbed open habitats	Single, stiff, obovate	2	Sept-Oct	May	HBG 135541
	Combretum zeyheri Sond.	tree	forest edges and open forest	Single, elliptic to obovate	8 or more	Sept-Oct	Aug-Sept	HBG 132510
Fabaceae-	*Cryptosepalum exfoliatum* De Wild.	geoxyle	geoxylic grasslands	pinnate	0.05	evergreen	evergreen	HBG 132481

Detarioideae	subsp. *suffruticans* (P.A.Duvign.)		on ferrallitic soils					HBG132754
	Cryptosepalum exfoliatum De Wild. subsp. *pseudotaxus* (Baker f.) P.A.Duvign. & Brenan	tree	top-slopes and plateau	Pinnate	12 or more	evergreen	evergreen	HBG 135304
	Brachystegia russelliae I.M.Johnst.	geoxyle	geoxylic grasslands on ferrallitic soils	large pinnate leaves with a stiff texture	0.3 -0.4	Aug-Sept	May-July	HBG 132793 HBG 143837
	Brachystegia longifolia Benth.	tree	forest-grassland-ecotones	large pinnate leaves with a stiff texture	15 or more	Sept-Oct	July-Aug	HBG 132957 HBG 134288 HBG 135621
Phyllanthaceae	*Uapaca nitida* Müll. Arg.var. *suffrutescens P.A.Duvign.*(2)	geoxyle	upper zone of geoxylic grasslands on ferrallitic soils	leathery lanceolate	0.4	evergreen	evergreen	HBG 132490 HBG 134199
	Uapaca nitida Müll. Arg.	tree	top-slopes and plateau	leathery lanceolate	10	evergreen	evergreen	HBG 135302

(1) *Syzygium guineense* (Willd.) DC. subsp. *macrocarpum* (Engl.) F. White is an evergreen that occurs in the study area in two different life forms. It can be found in the geoxyle - grasslands on the lower slopes as a suffrutex, flowering and fruiting in this stage. Vertical shoots are periodically killed by night frost in the dry season and removed by subsequent fires. In close proximity to the geoxylic grasslands, but a bit further toward the topslopes, the same taxon is growing as a low multistemmed subcanopy tree in an open woodland environment. Protected from night frost by the canopy of the dominant tree species (i.e. *Brachystegia spiciformis* and *Cryptosepalum exfoliatum* ssp. *pseudotaxus*), die-backs appear to be less frequent and fire-frequency and intensity are much lower in the woodland habitats (Stellmes et al., 2013). However, the population of *Syzygium guineense* subsp. *macrocarpum* in the grassland habitats is in contact with the obligate *Syzygium guineense* (Willd.) DC. subsp. *huillense* (Hiern) F.White growing along wetland borders. Zigelski et al. (2018) showed that gene flow between *Syzygium guineense* subspecies is common along contact zones of populations. Thus, it cannot be excluded that the geoxyle population of *Syzygium guineense* subsp. *macrocarpum* analyzed in this study represents a hybrid population with *Syzygium guineense* subsp. *huillense*.

(2) *Uapaca nitida* var *suffrutescens* is not listed in the catalogue of Angolan plants by Figueiredo and Smith (2008). The description of this taxon by Duvigneaud fits well to our *taxon*, however we are sure it needs supspecies or species status due to the notable differences to *Uapaca nitida*. It is also referred to as an only rhizomatous species of the *Uapaca* genus in Angola with a limited distribution, only known in some zones of the Bié province, to the east of the Cuanza River, extending, possibly, to Moxico province in similar ecological conditions" (Santos, 1967).

Table S7: Mean values of plant traits for all species refered in chapter 2. SLA- Specific Leaf Area; LT- Leaf Thickness; WD- Wood Density; LN- Leaf Nitrogen Concentraition; LC- Leaf Carbon Concentraition; LP- Leaf Phosphorous Concentraition; LCa- Leaf Calcium Concentraition; LMg- Leaf Magnesium Concentraition; LK- Leaf Potassium Concentraition; LWP- Leaf Water Potential. Species: Brs-*Brachystegia russelliae*; Blf-*Brachystegia longifolia*; Cef-*Cryptosepalum exfoliatum* subsp. *pseudotaxus*; Cpt-*Combretum platypetalum*; Csf-*Cryptosepalum exfoliatum* subsp. *suffruticans*; Pcp-*Parinari capensis*; Pcr-*Parinari curatelifolia*; Szs-*Syzygium guineense* subsp. *huilense*; Szt-*Syzygium guineense* subsp. *macrocarpum*; Uns-*Uapaca nitida* var. *suffrutescens*; Unt-*Uapaca nitida* subsp. *nitida*.

Life form	species	SLA	LT	WD	LN	LC	LP	LCa	LMg	LK	LWP
Geox.	Brs	93.60	0.22	0.70	1.93	52.73	1.54	9.36	5.05	2.20	-10.6
	Csf	109.43	0.20	0.62	2.22	46.26	1.52	6.91	5.77	2.23	-10.6
	Uns	78.87	0.39	0.62	1.52	49.05	0.82	2.19	0.16	9.81	-6.5
	Pcp	72.76	0.26	0.55	1.35	45.51	0.75	3.07	0.15	9.10	-10.7
	Szs	65.12	0.37	0.53	1.17	51.78	0.81	4.44	4.58	2.24	-9.2
	Cpt	70.16	0.35	0.71	1.12	48.50	0.75	3.39	0.15	9.70	(1)
trees	Blf	98.98	0.20	0.58	2.09	54.50	1.44	4.91	0.81	10.90	-11.0
	Cef	95.74	0.25	0.54	2.40	52.00	1.12	2.47	0.22	10.40	-10.0
	Unt	80.43	0.34	0.49	1.60	49.76	1.14	4.96	0.23	9.95	-2.8
	Pcr	54.66	0.38	0.47	1.05	40.86	0.58	6.57	0.12	8.17	-7.0
	Szt	67.47	0.32	0.55	1.17	51.78	0.71	6.40	0.14	10.36	-5.3
	Czh	100.07	0.30	0.65	2.25	50.50	1.51	7.86	0.30	10.10	-10.1

(1) Trait not measured because of the early leaf sheading in the dry season.

Table S8: PCA eigenvalue and % of variation explained by each PC in the chapter 2.

PC	Eigenvalue	% variance
1	4.07976	45.331
2	1.85697	20.633
3	0.952487	10.583

Table S9: One-way ANOVA showing traits variation in ectomycorrhizal (ECM) and non ectomicorrhizal (non-ECM) species.

	Traits	**Mean±se ECM**	**Mean±se non-ECM**	**One-way ANOVA**	
				F	**p(same)**
geoxyles	SLA (cm^2/g)	93.97±3.89	67.79±2.23	34.14	***
	LT (mm)	0.270±0.02	0.380±0.01	15.53	***
	LA (cm^2)	51.22±11.25	109.62±7.3	16.83	***
	LDMC (mg/g)	0.427±0.02	0.432±0.02	0.01	n.s.
	WD (g/cm^3)	0.647±0.04	0.607±0.01	1.36	n.s.
	LN (%)	1.89±0.09	1.39±0.06	18.37	***
	LC (%)	49.35±0.7	49.64±0.4	0.14	n.s.
	LP (mg/g)	1.29±0.09	0.83±0.04	26.44	***
	LCa (mg/g)	6.15±0.8	5.94±0.6	0.04	n.s.
	LMg (mg/g)	3.66±0.7	1.40±0.4	8.74	***
	LK (mg/g)	4.75±0.96	8.39±0.46	13.98	***
	C:N ratio	26.98±1.26	39.20±1.96	12.24	***
	N:P ratio	15.33±0.79	17.62±0.81	2.39	n.s.
	WP (bar)	-9.25±0.5	-6.45±0.6	7.73	***
Trees	SLA (cm^2/g)	87.26±1.66	79.27±3.02	5.39	***
	LT (mm)	0.253±0.007	0.300±0.01	14.39	***
	LA (cm^2)	125.97±12.25	110.79±8.52	1.04	n.s.
	LDMC (mg/g)	0.47±0.01	0.45±0.01	1.60	n.s.
	WD (g/cm^3)	0.537±0.008	0.580±0.013	8.31	***
	LN (%)	1.97±0.06	1.98±0.12	0.00	n.s.
	LC (%)	51.51±0.47	50.55±0.81	1.08	n.s.
	LP (mg/g)	1.21±0.03	1.02±0.06	7.49	***
	LCa (mg/g)	4.60±0.27	5.52±0.39	3.78	n.s.
	LMg (mg/g)	0.32±0.09	0.20±0.01	1.52	n.s.
	LK (mg/g)	10.30±0.09	10.11±0.2	1.08	n.s.
	C:N ratio	26.85±0.7	29.63±2.1	1.56	n.s.
	N:P ratio	16.54±0.57	19.61±0.75	10.65	***
	WP (bar)	-10.80±0.77	-7.78±0.54	10.26	***

Significant differences ($p<0.05$) are marked with ***. n.s.=no significant differences.

Table S10: General data of PFT for geoxyles. Adm-*Adenodolichos mendesii*; Ast-*Annona stenophylla*; Brs-*Brachystegia russelliae*; Ces-*Cryptosepalum exfoliatum* subsp. *suffruticans*; Cpt-*Combretum platypetalum*; Oar-*Ochna arenaria*; Pcp-*Parinari capensis*; Ptr-*Protea trichophylla*; Pzh-*Pygmaeothamnus zeyheri*; Rex-*Rhus exeliana*; Shl-*Syzygium guineense* subsp. *huilense*; Uns-*Uapaca nitida* var. *suffrutescens*. Extreme values (min. and max.) of each trait are in bold on the upper part of the table.

	SLA	**LT**	**LA**	**LDMC**	**WD**	**LN**	**LC**	**LP**	**LCa**	**LMg**	**LK**	**C/N**	**N/P**	**WP**
Adm	95.43	**0.53**	**189.8**	**0.2**	**0.51**	2.14	48.95	1.38	7.2	6.93	3.99	22.31	16.82	**-1.52**
Ast	80.52	0.4	99.71	0.31	0.54	1.6	48.63	1.07	9.59	0.21	9.71	30.47	15.77	-4.18
Brs	93.6	0.22	45.14	0.49	0.7	1.95	**52.61**	**1.57**	9.36	5.05	**2.2**	27.46	**12.6**	-10.6
Ces	**109.43**	**0.2**	**4.42**	0.47	0.62	**2.15**	45.42	1.46	6.91	5.77	2.23	**21.27**	14.82	-10.64
Cpt	70.16	0.35	143.12	0.4	0.71	1.12	48.37	0.76	3.39	0.15	9.7	43.9	14.9	*
Oar	58.72	0.27	101.31	**0.63**	0.68	1.35	52.58	0.57	4.2	0.13	**10.46**	39.54	**25.5**	**-11.71**
Pcp	72.76	0.26	31.77	0.53	0.55	1.46	**42.54**	0.74	3.07	0.15	9.1	33.77	17.96	-10.65
Ptr	**44.63**	0.53	86.74	0.43	0.63	**0.78**	51.2	**0.5**	2.34	0.1	10.3	**68.85**	14.92	-4.43
Pzh	63.64	0.33	69.96	0.52	**0.71**	1.4	51.73	0.61	5.27	0.13	10.06	37.71	22.3	-7.55
Rex	59.12	0.37	93.69	0.45	*	1.72	49.63	0.96	**13.91**	0.2	9.93	31.46	15.92	-2.32
Shl	65.12	0.37	170.47	0.41	0.53	1.2	51.67	0.8	4.44	4.58	2.24	44.76	14.52	-9.23
Uns	78.87	0.39	104.1	0.32	0.62	1.55	49.15	0.82	**2.19**	0.16	9.81	32.22	18.56	-6.52
Mean	74.33	0.35	95.02	0.43	0.62	1.54	49.37	0.94	5.99	1.96	7.48	36.14	17.05	-7.21
Std. err.	5.28	0.03	15.7	0.03	0.02	0.12	0.87	0.1	1.02	0.79	1.04	3.67	1.05	1.1
Std. dev.	18.3	0.11	54.38	0.11	0.08	0.41	3	0.36	3.55	2.73	3.6	12.72	3.63	3.65
Variance	334.88	0.01	2957.2	0.01	0.01	0.019	5.19	0.12	12.59	7.43	12.96	161.9	13.21	13.32
Min.	44.63	0.2	4.42	0.2	0.51	0.78	42.54	0.5	2.19	0.1	2.2	21.27	12.6	-11.7
Max.	109.43	0.53	189.8	0.63	0.71	2.15	52.61	1.57	13.91	6.93	10.46	68.85	25.5	-1.52

*- not measured

Table S11: General data of PFT for trees. Baf-*Burkea Africana*; Bbk-*Brachystegia bakeriana*; Bbq-*Baphia bequaertii*; Blf-*Brachystegia longifolia*; Bsp-*Brachystegia spiciformis*; Cef-*Cryptosepalum exfoliatum* subsp. *pseudotaxus*; Czh-*Combretum zeyheri*; Eaf-*Erytrophleum africanum*; Jpn-*Julbernardia paniculata*; Maf-*Monotes africanus*; Pcr-*Parinari curatellifolia*; Png-*Pterocarpus angolensis*; Szt-*Syzygium guineense* subsp. *guineense*; Unt-*Uapaca nitida* subsp. *nitida.* Extreme values (min. and max.) of each trait are in bold on the upper part of the table.

	SLA	**LT**	**LA**	**LDMC**	**WD**	**LN**	**LC**	**LP**	**LCa**	**LMg**	**LK**	**C/N**	**N/P**	**WP**
Baf	71.54	0.301	90.84	0.47	0.62	2.07	**54.74**	0.81	3.32	0.16	**10.95**	26.69	**25.48**	-10.9
Bbk	76.58	0.258	61.39	0.51	0.55	1.95	54.13	1.16	**4.98**	0.23	10.83	28.01	16.82	-11
Bbq	77.26	0.358	32.71	0.37	**0.66**	2.7	50.9	1.27	3.64	0.25	10.18	19.14	21.33	-8.59
Blf	98.98	**0.203**	**209.25**	0.5	0.58	2.09	54.5	1.44	4.91	**0.82**	10.9	26.16	14.6	-11
Bsp	89.15	0.226	156.82	0.5	0.53	2.01	49.13	1.44	5.13	0.29	9.83	24.45	14.05	-10.5
Cef	95.74	0.252	**7.13**	0.42	0.54	2.4	52	1.12	**2.47**	0.22	10.4	21.8	21.88	-10.3
Czh	100.07	0.299	156.92	**0.34**	0.65	2.25	50.5	**1.51**	**7.86**	0.3	10.1	22.53	15.09	-10.1
Eaf	82.46	0.236	57.86	0.52	0.6	1.99	54.35	0.84	3.54	0.17	10.87	27.44	23.82	-10.9
Jpn	86.98	0.25	190.61	0.46	0.51	2.24	52.41	1.18	6.31	0.24	10.48	23.48	19.39	-10.8
Maf	82.97	0.238	114.5	**0.52**	0.55	1.49	48.67	1.01	3.41	0.2	9.73	32.87	14.79	**-19.4**
Pcr	**54.66**	**0.378**	126.46	0.49	**0.47**	1.05	**40.86**	**0.58**	6.57	**0.12**	**8.17**	39.17	20.08	-6.98
Png	**101.46**	0.208	145.49	0.48	0.51	**2.81**	50.91	1.42	7.31	0.28	10.18	**18.19**	18.1	**-1.74**
Szt	67.47	0.321	165.23	0.46	0.55	**0.96**	51.58	0.71	6.4	0.14	10.32	**54.27**	**13.4**	-5.3
Unt	80.43	0.345	142.11	0.36	0.49	1.6	49.76	1.14	4.96	0.23	9.95	31.17	14.22	-2.75
Mean	83.27	0.28	118.38	0.46	0.56	1.97	51.03	1.12	5.06	0.26	10.21	28.24	18.08	-9.29
Std. err.	3.6	0.02	16.14	0.02	0.02	0.15	0.95	0.08	0.44	0.05	0.19	2.49	1.06	1.15
Std. dev.	13.47	0.06	60.38	0.06	0.06	0.54	3.55	0.29	1.65	0.17	0.71	9.32	3.97	4.29
Variance	181.5	0.00	3645.7	0.00	0.00	0.03	12.62	0.09	2.72	0.03	0.50	86.89	15.76	18.44
Min.	54.66	0.2	7.13	0.34	0.47	0.96	40.86	0.58	2.47	0.12	8.17	18.19	13.4	-19.4
Max.	101.46	0.38	209.25	0.52	0.66	2.81	54.74	1.51	7.86	0.82	10.95	54.27	25.48	-1.74

Declaration of oath

I hereby declare on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, den	Unterschrift
18/03/2021	Amândio Luís Gomes

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TO WHOM IT MAY CONCERN

As a native English speaker and experienced proof-reader, I hereby declare that the PhD thesis “How root morphology and functional traits enable geoxyles to thrive in nutrient poor and disturbance prone Angolan miombo ecosystems” has been written in correct and concise British English.

Yours sincerely,

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