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Vegetation description around the savanna flux measurement site at Benfontein Nature Reserve, South Africa



Buster Mogonong^{a,b,*}, Helga van der Merwe^{a,c}, Tshililo Ramaswiela^a, Amukelani Maluleke^d, Gregor Feig^{a,e}

^a South African Environmental Observation Network (SAEON), P.O. Box 2600, Pretoria 0001, South Africa

^b Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg 2050, South Africa

^c Department of Biological Sciences, Plant Conservation Unit, University of Cape Town, Rondebosch 7700, South Africa

^d Department of Botany & Zoology, Stellenbosch University, Stellenbosch, South Africa

^e Department of Geography, Geoinformatics and Meteorology, University of Pretoria, South Africa

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ABSTRACT

A flux tower with eddy covariance instruments was recently erected at Benfontein Nature Reserve (BNR) outside of Kimberley. An understanding of the landscape within the flux tower footprint, in this case natural vegetation, is necessary to interpret the data collected by the eddy covariance instruments. The tower was erected as part of the Expanded Freshwater and Terrestrial Environmental Observation Network (EFTEON) infrastructure initiative to establish long-term monitoring platforms focused on socially relevant terrestrial landscapes and their coupled hydrological systems. We sought to describe the vegetation within the flux tower footprint to set a baseline of the vegetation in the landscape at the inception of the long-term monitoring of flux measurements at BNR. Woody vegetation was surveyed in five square 1 ha plots while the herbaceous layer was sampled across 105 circular plots following the Socio-Ecological Observatory for Southern African Woodland (SEOSAW) protocol. Woody vegetation was quantified in terms of abundance, diversity and biomass, together with Size Class Distribution (SCD) methods to describe the woody vegetation structure. The herbaceous layer was described by species count, basal cover, biomass, and diversity which was assessed using the Shannon-Weiner Diversity Index. Five tree species, dominated by Vachellia erioloba, were found in the plots. Recruits (0 and 1 m tall) were significantly more abundant than large trees (1.2–9.5 m high). The SCD for the woody vegetation yielded a Type IIIa curve i.e. populations missing one or more size classes, for all tree species except Ziziphus mucronata which yielded a Type IIIb curve representing a population missing small sized trees. The herbaceous layer was diverse, consisting of 10 grass and 32 forb species. Schmidtia pappophoroides was the dominant grass species in terms of count, basal cover and aboveground biomass. Herbaceous biomass was two times higher than that of woody vegetation, with the North plot contributing the highest biomass for herbaceous and woody vegetation. The results indicate that the vegetation around the flux tower represents a wooded grassland, which is a type of a savanna. These vegetation data will contribute to the interpretation of data collected by the flux tower instruments now and in the future. Furthermore, long-term data collection in this reserve is needed to capture the woody vegetation dynamics and its interaction with the herbaceous layer.

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1. Introduction

Vegetation plays a vital role in influencing landscape processes such as acting as carbon sinks (Fang et al., 2007), supporting herbivores, and preventing soil erosion (Sala and Paruelo, 1997). Moreover, vegetation provides essential ecosystem services, such as the

E-mail address: b.p.mogonong@gmail.com (B. Mogonong).

provisioning of non-timber forest products that are crucial for sustaining livelihoods (Shackleton and Shackleton, 2004). Describing and characterizing vegetation structure and diversity is therefore crucial for long-term studies, including those which seek to understand the interaction between atmospheric and terrestrial processes or the long-term impact of climatic, hydrological, and land use change drivers (Palmer et al., 2015).

Size class distribution (SCD) methodology as a proxy of woody vegetation community structure has been successfully used in various studies in the past (Condit et al., 1998; Gaugris and Van Rooyen,

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^{*} Corresponding author at: South African Environmental Observation Network (SAEON), P.O. Box 2600, Pretoria 0001, South Africa.

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2007; Van der Merwe et al., 2019). These studies showed that population characteristics such as structure, health, and direction (growth or decline) can be determined from SCD analyses. Attributes such as tree height and stem diameter are commonly used in SCD analysis. Tree height can be affected by diebacks due to frost, herbivory, and fire (Muller et al., 2016), resulting in increased variability. However, tree height is still a useful variable in understanding woody vegetation structure.

Woody vegetation structure has been widely studied in South Africa (Van der Walt and Le Riche, 1984; Gaugris and Van Rooyen, 2007; Seymour, 2008, 2009; Van der Merwe et al., 2019). In the arid region, numerous studies on woody vegetation structure have been conducted in the Kalahari region in the Northern Cape province (Scholes et al., 2002; Van der Merwe et al., 2019). Usually, studies only focus on the population structure of single species rather than a comparison among multiple woody plants, with most attention being given to the keystone species (Steenkamp et al., 2008), Vachellia erioloba, and its interaction with plant communities (Seymour, 2009).

In savanna ecosystems, woody and herbaceous vegetation coexist, resulting in a matrix of grasses, forbs and trees/shrubs. The interaction between grasses and trees is competitive in nature, whereby high tree cover leads to reduced grass biomass (Richter et al., 2001). The herbaceous layer is often characterized and described by species counts and biomass estimations using measuring equipment such as disk pasture meters (Richter et al., 2001; Masunga et al., 2013) or the clipping and weighing of dried grass and forb material (Scholes et al., 2001).

Vegetation change is driven by various factors such as climate, water availability, land use change, fire, and herbivory (Bond and Midgley, 2012; Devine et al., 2017). Studies have shown a positive link between increased woody vegetation biomass and carbon dioxide (CO₂) across Africa (Stevens et al., 2017). Bush encroachment was observed to not necessarily affect the species composition of the herbaceous layer, even though it does have effects on the density, production and grazing capacity (Richter et al., 2001). Other studies have shown that fire and herbivory may reduce tree dominance in South African savannas (Higgins et al., 2000; Langevelde et al., 2003; Stevens et al., 2016) while also reducing the species diversity between communities of herbaceous vegetation (Masunga et al., 2013). While fire may increase vegetation mortality and reduce tree basal area (Lehmann et al., 2014), it also reduces self-shading and competitive pressure, which has a positive indirect effect on plant fitness (Zimmermann et al., 2010). Furthermore, herbivory influences species composition of particularly the herbaceous layer. Studies have shown that in semi-arid regions, high grazing intensity leads to reduced productivity and abundance of perennial grasses (Pfeiffer et al., 2019).

The recently established Socio-Ecological Observatory for the Southern African Woodlands (SEOSAW) protocols aim for long-term woody and herbaceous vegetation surveys to be standardized across savannas, dry forests, and thickets (The SEOSAW partnership, 2020). Data collected following this protocol provides an opportunity to assess various ecological processes such as vegetation change over time and can also be used to ground truth remote sensing data. Data from the SEOSAW initiative have been used in various studies where ecological processes in woodlands across African countries, including South Africa, were assessed (McNicol et al., 2018; Fayolle et al., 2019; Godlee et al., 2020). A key feature of the protocol is that it includes aspects of composition (number of species), structure (morphology and signs of use or damage) and demographics (size classes), which allows the measurement of aspects such as population structure, use and biomass.

In November 2019, a paired set of eddy covariance instruments was set up at Benfontein Nature Reserve under the auspices of the Expanded Freshwater and Terrestrial Environmental Observation Net work (EFTEON) Research Infrastructure (Feig, 2018). The towers were established in the Savanna and a patch of Karoo vegetation. The flux

towers are equipped with eddy covariance instrumentation for the measurement of the exchange of CO₂ and water vapor (IRGASON), atmospheric pressure, temperature and humidity, photosynthetically active radiation, precipitation, wind speed and direction, net radiation, soil moisture across the 25-75 mm depth and at 300 mm, the soil heat flux and soil temperature. To fully understand and interpret the parameters measured by the eddy covariance instruments, a detailed vegetation survey around the footprint of the flux tower is important since vegetation influences a portion of what is being measured by the instruments (Williams et al., 2012). Moreover, changes in the parameters measured by the flux tower over the long-term may lead to changes in the vegetation structure, diversity and biomass of the landscape. For instance, an increase in CO₂ may lead to increased woody vegetation (Stevens et al., 2017). Vegetation is also likely to respond positively (i.e. increase in biomass) during periods of increased precipitation and soil moisture (Berry and Kulmatiski, 2017). Soil moisture is tipped to be a limiting factor for vegetation dynamics, particularly production, in drier areas such as BNR (Cleverly et al., 2016).

We implemented the SEOSAW protocol around the EFTEON savanna flux tower as an initiative that forms part of establishing long-term vegetation monitoring plots at BNR. We sought to describe the vegetation within 250–300 m of the flux tower footprint to set a baseline for the vegetation in the landscape on the inception of the long-term monitoring of flux measurements at BNR. We achieved this by assessing the woody vegetation structure (using SCD), abundance, diversity, and biomass, while describing herbaceous species abundance, basal cover, biomass and diversity. Basic vegetation information will be required by the scientists using the data collected by the eddy covariance instruments and this paper seeks to provide that information.

2. Methods

2.1. Study site

The study was conducted in the BNR in South Africa (Fig. 1). This reserve is owned by De Beers Consolidated Mines and was established in 1891. At approximately 11 000 ha in size, the reserve is located where the Nama-Karoo (Northern Upper Karoo), Savanna (Kimberley Thornveld) and Grassland biomes meet (Mucina and Rutherford, 2006). The land was initially purchased as a potential mining site, however, it is now dedicated to wildlife conservation. Semi-arid climatic conditions prevail, with a mean annual rainfall of 419 ± 134 mm (Kamler et al., 2012). Thunderstorms are common in summer and frost in winter. The Thornveld vegetation is an open savanna system dominated by grasses (such as Schmidtia pappophoroides and Stipagrostis uniplumis) and forbs (e.g. Selago dinteri, Wahlenbergia spp.) (Mucina and Rutherford, 2006). Tree species such as V. erioloba, Vachellia tortilis, Searsia lancea, and Senegalia mellifera are found in the matrix of grasses and forbs while shrubs such as Ziziphus mucronata, Ehretia rigida and Grewia flava are found mostly in clumps under large trees (Mucina and Rutherford, 2006).

2.2. Data collection

2.2.1. Woody vegetation

Plot design and data collection were done following the SEOSAW protocol, https://seosaw.github.io/manuals.html, thus we do not expand greatly on them. In 2021 we surveyed five square-shaped 1 ha plots placed in the four cardinal directions, and one plot at the center at the savanna flux tower (Fig. 1). The plots in the four-cardinal directions were centered 100 m away from the tower to cover the radius of the flux tower footprint.

We recorded woody plant species to investigate diversity and the number of individual trees to account for abundance per species. For



Fig. 1. Benfontein Nature Reserve (B) in South Africa (A). Plot design and location of the Expanded Freshwater and Terrestrial Environmental Observation Network (EFTEON) savanna flux tower (C). The labels in the plot represent: N- North plot, S- South plot, E- East plot, W- West plot and C – Center plot.

each large tree (>1 m in height), stem circumference and tree height were measured. Tree height was measured using an extendable measuring rod, and stem circumference was measured using a tape measure at 300 mm above the soil surface. Recruits (0 and 1 m in height) with stem diameter of <50 mm were also sampled, however, only the height was measured for these individuals. Each large tree was marked with an aluminum metal tag and the location of all the trees was marked using a Global Positioning System (GPS) at an estimated accuracy level of 5 m.

2.2.2. Herbaceous vegetation

The SEOSAW protocol was also used to guide the herbaceous vegetation sampling. Grass and forb species were sampled across the same 1 ha plots that were used to sample the woody vegetation. A total of four 25 m transects running in four cardinal directions were established in each 1 ha plot. Similarly, to the placement of the woody vegetation plots, the transects were centered 100 m away from the flux tower. In each transect line, five circular plots of a 1 m radius were established 5 m apart from each other (refer to SEOSAW Grass sampling protocol for details). In each circular plot, diversity was assessed and basal cover estimated. For every center point of each transect (i.e. third plot) grasses and forbs were clipped in subplots with an area of 0.25 m² and dried to a constant mass and weighed to obtain dry biomass. A total of 105 circular plots were sampled and 25 subplots clipped to determine dry biomass.

2.3. Data analysis

2.3.1. Diversity, abundance, and height of woody species

Woody species abundance was calculated by adding the number of individuals for each species in the plots. Mean height was calculated at three levels (i.e. overall, large trees and recruits). 'Overall' mean height represents the average height of all individuals (recruits and large trees) per species in all the sampled plots. 'Large trees' mean height is the average height of all the large trees per species in the sampled plots. 'Recruits' mean represents the average height of all individuals per species between 0 and 1 m in height.

2.3.2. Population structure of woody species

Size class distribution (SCD) was used to examine the population structure of the species. However, the population structure of *Senegalia mellifera* could not be analyzed due to an insufficient number of individuals encountered in the plots. All the data were combined and SCD analysis was done using the totals per 5 hectares. The SCD was based on tree height and each species was assigned its own height categories since the maximum height varied between species. Most of the trees were in the 0 and 1 m class; thus, this range was further subdivided into finer categories in the following sequence: 0-0.1, >0.1-0.2, >0.2-0.3, >0.3-0.4, >0.4-0.5, >0.5-0.6, >0.6-0.7, >0.7-0.8, >0.8-0.9, >0.9-1, starting with class 1 and ending with class 10.

The population structure of each species was described and interpreted based on the four types of population curves defined by Gaugris and Van Rooyen (2007). Type I is an inverse J-shaped curve representing a growing population, dominated by small size trees with few large individuals. Type II represents an ideal population structure in which there are few small sized individuals. Type III is divided into Type IIIa and Type IIIb. The Type IIIa curve is similar to the Type I curve; however, the population is missing one or more size classes. Type IIIb represents a population that is missing small size classes and gaps where other size classes may be missing in the population. Type IV forms a bell-shaped curve with one or two peaks, representing an abnormal range of size classes.

2.3.3. Diversity, abundance, and basal cover of herbaceous species

A Shannon-Weiner Diversity Index (*H*) was used to calculate herbaceous species diversity. The index was calculated in R statistical software, using the Biodiversity function from the Vegan package (Oksanen et al., 2007). Shannon-Weiner Diversity Index is commonly used in many ecological studies to assess the biological diversity of a community (Di Bitetti, 2000).

Abundance of each species was calculated by adding the number of individuals for each species in the plots and mean count per species was calculated per hectare. Mean, standard deviation and error were calculated using Microsoft Excel for the basal cover of all the grass and forb species.

2.3.4. Biomass estimates

Aboveground biomass (AGB) was estimated for both herbaceous and woody vegetation. Woody vegetation AGB was estimated per plot using an allometric equation by Chave et al. (2014). This equation uses tree height, diameter and wood density as key variables that influence the biomass of trees. Tree stems with a diameter of less than 50 mm were excluded from the tree biomass estimation. Herbaceous vegetation biomass was estimated by drying and weighing the clipped grass and forb material. The clipped material was collected in brown paper bags and dried in an oven at 60 °C for 24 h before being weighed on a digital scale. Herbaceous biomass was estimated by converting the weighed grass and forb material to mass per unit area (tons/ha).

Overall, the herbaceous and woody vegetation yielded data that were not normally distributed, and a Wilcoxon signed rank test was used to assess the differences in biomass contribution. Analysis of variance (ANOVA) was used to test for significant differences in biomass contribution among the 1 ha plots for both the woody and herbaceous vegetation. A Tukey Honest Significant Difference (TukeyHSD) was used to further interrogate mean biomass difference between plots. The statistical analysis was all done in R statistical software using the stats package.

3. Results

3.1. Diversity, abundance, and height of woody species

A total of 1007 individual trees (\sim 200/ha) consisting of five species (*V. erioloba, V. tortilis, Searsia lancea, Z. mucronata* and *Senegalia mellifera*) were recorded in the five 1 ha plots. Most (95.9 %) of the individuals were recruits while 4.1 % were large trees. *Vachellia erioloba* had the highest tree height for the large trees while *Searsia lancea* had a higher overall mean height (Table 1). Only one large individual of *V. tortilis* was found in the sampled plots and only three *Senegalia mellifera* individuals, thus mean height could not be calculated for these two species.

3.2. Population structures of woody vegetation

The overall height SCD curves indicated a large number of individuals in the size class that was less than 1 m tall and sharply declined as the height classes increased (Fig. 2A). The pattern resembles a Type IIIa population structure for *V. erioloba*, *V. tortilis* and *Searsia lancea* while *Z. mucronata* resembles a Type IIIb. The size class distribution of individuals that fell within the 0 and 1 m recruiting group yielded Type IIIb population structure curves for all the tree species (Fig. 2B).

3.2.1. Diversity and abundance of herbaceous vegetation

A total of 10 grass and 32 forb species were found in the sampled plots. Of the 32 forb species, seven were unidentified due to the lack of identifiable features in these species at the time of the survey. Such species are indicated by a collector's name i.e. TRBM followed by a specimen collection number. *Schmidtia pappophoroides* was most abundant when compared to all the other grass and forb species (Supplementary Table 1).

The Shannon-Weiner Diversity Index (H) indicated that the sampled plots were diverse. Comparison of diversity among the sampled plots showed the North (H = 1.7), West (H = 1.6) and Center (H = 1.6) plots had a higher diversity compared to the East (H = 1.2) and South (H = 1.1) plots.

3.3. Basal cover

Schmidtia pappophoroides had the highest basal cover compared to all other grass species in the sampled plots, with an average of 9.96 % (Table 2). The second highest basal cover was for *Stipagrostis uniplumis* with a distinctly lower 2.73 % average basal cover. Forb species contributed an average of 0.2 % to the overall herbaceous basal cover in the sampled plots.

3.4. Biomass estimates

Overall, the herbaceous vegetation contributed an average of 1.50 ± 2.20 tons/ha of AGB to the sampled site while woody vegetation contributed 0.74 ± 0.78 tons/ha. Herbaceous contribution to AGB was higher than that of the woody vegetation, however, this difference was not significant (W = 1633.5, p > 0.05). Of both woody and herbaceous vegetation, *V. erioloba* and *Schmidtia pappophoroides* contributed the most to the AGB respectively (Supplementary Tables 2 and 3).

At plot level, there was no significant difference in mean AGB for woody vegetation (F = 2.473, df = 4, p > 0.05), however, a TukeyHSD post hoc analysis showed that the North plot (1.84 ± 1.09 tons/ha) had a significantly higher mean woody biomass compared to the East plot (0.44 ± 0.69 tons/ha) (p < 0.05) (Fig. 3A). The herbaceous dry biomass was not significantly different across all the plots despite having a higher contribution from the North plot (F = 0.732, df = 4; p > 0.05) (Fig. 3B).

Table 1

Mean height (m) for each woody species found at the Expanded Freshwater Terrestrial Environmental Observation Network (EFTEON) savanna flux tower site at Benfontein Nature Reserve, South Africa.

| Species name | Total number of individuals | Mean height (m) | | |
|---------------------|--------------------------------|------------------------------------|---------------------------------|------------------------------|
| | | Overall (large trees and recruits) | Large trees (>1 m in height) | Recruits (<1 m in height) |
| Vachellia erioloba | 520 | 0.49 | 6.39 | 0.15 |
| Vachellia tortilis | 391 | 0.22 | - | 0.21 |
| Ziziphus mucronata | 58 | 0.40 | 2.70 | 0.23 |
| Searsia lancea | 35 | 0.63 | 2.27 | 0.22 |
| Senegalia mellifera | 3 | - | - | - |

- not calculated.



Fig. 2. Height class distribution of four species per five hectares at Benfontein Nature Reserve, South Africa. The set of four curves in (A) shows the overall height distribution of all trees while (B) shows height distribution of recruits (<1 m in height).

Table 2

Rooted basal cover (%) contribution by herbaceous species sampled at Benfontein savanna site, Benfontein Nature Reserve, South Africa.

| Species | Basal cover (%) | | |
|--------------------------------------|-----------------|-------|------|
| | Mean | SD | SE |
| Schmidtia pappophoroides | 9.96 | 6.61 | 0.66 |
| Stipagrostis uniplumis | 2.73 | 2.13 | 0.41 |
| Pogonarthria squarrosa | 1.49 | 1.11 | 0.19 |
| Aristida congesta subsp. congesta | 0.73 | 0.98 | 0.34 |
| Eragrostis lehmanniana | 2.44 | 1.93 | 0.27 |
| Bulbostylis hispidula | 0.36 | 0.31 | 0.08 |
| Aristida congesta subsp. barbicollis | 1.52 | 0.97 | 0.43 |
| Heteropogon contortus | 2.00 | - | _ |
| Setaria verticillate | 0.13 | 0.06 | 0.03 |
| cf. Brachiaria nigropedata | 0.10 | - | _ |
| Forbs | 0.22 | 0.50 | 0.03 |
| Total | 21.67 | 14.58 | 2.45 |

4. Discussion

The vegetation around the EFTEON flux tower can be described as a sparsely wooded grassland, which is a type of savanna. The landscape consists of a well-developed layer of herbaceous vegetation and sparsely distributed woody vegetation. Woody species richness in the plots around the flux tower consisted of five tree species, with *V. erioloba* being the dominant and most abundant tree followed by *V. tortilis.* Although the latter had a high number of individuals, only one large tree was present in the South plot. The species found in the plots represent the semi-arid savanna trees at BNR (Seymour, 2008). However, some other common shrub species such as E. rigida and G. flava were not found in the sampled plots. Ehretia rigida and G. flava were observed to occur \sim 300 m away to the south of the sampled plots, raising questions regarding the recruitment, seed dispersal and climatic conditions suitable for the survival of these species. Both these species are palatable to browsers including cattle and antelope (Owen Smith and Cooper, 1987). Their absence may be related to land use history. The presence, sometimes at high densities, of Datura ferox below larger trees also indicates herbivore trampling and



Fig. 3. Mean biomass (± SD) of (A) woody and (B) herbaceous vegetation at 1 ha plot level at Benfontein savanna site, Benfontein Nature Reserve, South Africa. Letters indicate significant differences between the plots.

dunging in shade patches. Furthermore, the absence of *E. rigida* and *G. flava* in our plots may be due to subtle differences in soil depth as well as nutrient and water availability, which requires further investigation.

All tree species yielded Type IIIa curves except Z. mucronata which exhibited a Type IIIb curve. Type IIIa curves are considered to show periodic and irregular seedling establishment that is driven by rainfall and herbivory and/or the impact of fire on the individual small trees (Gaugris and Van Rooven, 2007), which is common for longlived woody plants in semi-arid regions (Schweiger et al., 2020). Furthermore, Type IIIa curves can also represent populations that are heavily disturbed through harvesting, lack of pollinators and seed dispersal agents, and suffer from the destruction of seedlings by animals (Peters, 1996). The BNR is a protected area, thus harvesting of trees in recent time would not affect the seedling establishment nor the large tree population, however, it is unknown if harvesting took place in the past given that V. erioloba provides quality fuelwood. Natural processes such as competition for water, herbivory, land use and fire drive the population structure in the reserve (Seymour and Huyser, 2008). Recruits, it is postulated, invest in capturing resources to then shoot out of the fire trap and outgrow grasses and other tree individuals into adulthood (Bond and Midgley, 2000). However, a study by Seymour et al. (2022) at BNR showed that over a 15-year period, V. erioloba saplings' mean height only increased by 45.4 mm, suggesting that this woody species can sometimes be trapped in the sapling stage for a long time before becoming large trees.

Fire has been actively excluded in the BNR with only infrequent fires occurring. The most recent fires (prior to sampling) occurred in September 2019, burning a portion of the South and East plots in our study area before sampling. On 28 September 2021, a large fire swept through the area after the sampling for this study had been concluded. None of the trees experienced fatal damage from the 2019 fire, however, the 2021 fire killed some of the large trees (*pers. obs.*) and a further significant fire occurred on the 9th of September 2023, with further large tree mortality expected.

The herbaceous vegetation was diverse across all the sampled plots, indicated by the Shannon-Weiner Diversity Index values of greater than 1. The dominant and most common grass species was *Schmidtia pappophoroides* which also had the highest mean basal cover, followed by *Stipagrostis uniplumis*. Basal cover is deemed to be a good index for dominance as it directly links to both biomass and peak leaf area (Scholes et al., 2001).

Following a good rainfall year, the standing mean AGB at the Benfontein was $1.22 (\pm 1.85 \text{ tons/ha})$, which is below the AGB estimated in other parts of South African savannas (Nickless et al., 2011; Odipo et al., 2016). Low AGB is typical for low vegetation areas, particularly grass or shrubs (Odipo et al., 2016), and the savanna flux tower is located in such a landscape where large trees are sparsely distributed in a grassy matrix, indicative of a wooded grassland. Amidst climate change where increased CO_2 promotes woody plant densification (Bond and Midgley, 2012), long-term monitoring is needed to track the changes in AGB at the site and the dynamics of *V. erioloba* as it is a keystone species, and if its population structure is altered it can lead to compositional and functional changes in savanna systems.

The mean ratio of woody to herbaceous biomass in the savanna system of the BNR is 0.74 ± 0.78 to 1.50 ± 2.20 tons/ha indicating the large contribution by the herbaceous layer to the AGB. This area is managed as a nature reserve where natural processes shape the landscape. Deviations in the woody to herbaceous biomass ratio may be indicative of disturbance such as woody encroachment, excessive grazing, or changes in amount and/or seasonality of rainfall.

5. Conclusion

We conclude that the EFTEON eddy covariance flux tower is located in a sparsely wooded grassland within the Savanna Biome, given that the herbaceous vegetation contributed more AGB when compared to the woody vegetation although the contributions were not significantly different. The system is dominated by the sparsely distributed tree, *V. erioloba*, and the abundant perennial grass *Schmidtia pappophoroides* which are the primary contributors to AGB. This vegetation description should contribute to an improved understanding and interpretation of eddy covariance instrument measurements now and in the future. Furthermore, our study sets a baseline for the long-term monitoring of woody and herbaceous vegetation at BNR.

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Declaration of Competing Interest

The authors of the manuscript would like to declare that there are no conflicts of interest, financial or otherwise associated with the manuscript.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.sajb.2023.09.010.

References

- Berry, R.S., Kulmatiski, A., 2017. A savanna response to precipitation intensity. PLoS One 12 (4), e0175402.
- Bond, W.J., Midgley, G.F., 2000. A proposed CO2-controlled mechanism of woody plant invasion in grasslands and savannas. Glob. Chang. Biol. 6, 865–869.
- Bond, W.J., Midgley, G.F., 2012. Carbon dioxide and the uneasy interactions of trees and savannah grasses. Philos. Trans. R. Soc. B Biol. Sci. 367, 601–612.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W., Muller-Landau, H., Mencuccini, M., Nelson, B., Ngomanda, A., Nogueira, E., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190.
- Cleverly, J., Eamus, D., Coupe, N.R., Chen, C., Maes, W., Li, L., Faux, R., Santini, N.S., Rumman, R., Yu, Q., Huete, A., 2016. Soil moisture controls on phenology and productivity in a semi-arid critical zone. Sci. Total Environ. 568, 1227–1237.
- Condit, R., Sukumar, R., Hubbell, S.P., Foster, R.B., 1998. Predicting population trends from size distributions: a direct test in a tropical tree community. Am. Nat. 152, 495–509.
- Devine, A.P., McDonald, R.A., Quaife, T., Maclean, I.M., 2017. Determinants of woody encroachment and cover in African savannas. Oecologia 183, 939–951.
- Di Bitetti, M.S., 2000. The distribution of grooming among female primates: testing hypotheses with the Shannon-Wiener diversity index. Behaviour 137, 1517–1540.
- Fang, J., Guo, Z., Piao, S., Chen, A., 2007. Terrestrial vegetation carbon sinks in China, 1981–2000. Sci. China Ser. D Earth Sci. 50, 1341–1350.
- Fayolle, A., Swaine, M.D., Aleman, J., Azihou, A.F., Bauman, D., Te Beest, M., Chidumayo, E.N., Cromsigt, J.P., Dessard, H., Finckh, M., Gonçalves, F.M.P., Gillet, J.F., Gorel, A., Hick, A., Holdo, R., Kirunda, B., Mahy, G., McNicol, I., Ryan, C.M., Revermann, R., Plumptre, A., Pritchard, R., Nieto-Quintano, P., Schmitt, C.B., Seghieri, J., Swemmer, A., Talila, H., Woollen, E., 2019. A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas. J. Biogeogr. 46, 454–465.
- Feig, G., 2018. The expanded freshwater and terrestrial environmental observation network (EFTEON). Clean Air J. 28.
- Gaugris, J.Y., Van Rooyen, M.W., 2007. The structure and harvesting potential of the sand forest in Tshanini Game Reserve, South Africa. S. Afr. J. Bot. 73, 611–622.
- Godlee, J.L., Gonçalves, F.M., Tchamba, J.J., Chisingui, A.V., Muledi, J.I., Shutcha, M.N., Ryan, C.M., Brade, T.K., Dexter, K.G., 2020. Diversity and structure of an arid woodland in Southwest Angola, with comparison to the Wider Miombo Ecoregion. Diversity 12, 140 (Basel).
- Higgins, S.I., Bond, W.J., Trollope, W.S.W., 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. J. Ecol. 88, 213–229.
- Kamler, J.F., Stenkewitz, U., Klare, U., Jacobsen, N.F., Macdonald, D.W., 2012. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. J. Wildl. Manag. 76, 1241–1253.
- Langevelde, F.V., Vijver, C.A.D.M.V.D., Kumar, L., Koppel, J.V.D., Ridder, N.D., Andel, J.V., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T., Rietkerk, M., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84, 337–350.
- Lehmann, C.E., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J., 2014. Savanna vegetation-fire-climate relationships differ among continents. Science 343, 548– 552.
- Masunga, G.S., Moe, S.R., Pelekekae, B., 2013. Fire and grazing change herbaceous species composition and reduce beta diversity in the Kalahari sand system. Ecosystems 16, 252–268.
- McNicol, I.M., Ryan, C.M., Mitchard, E.T., 2018. Carbon losses from deforestation and widespread degradation offset by extensive growth in African woodlands. Nat. Commun. 9, 1–11.
- Mucina, L., Rutherford, M., 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

- Muller, K., O'Connor, T.G., Henschel, J.R., 2016. Impact of a severe frost event in 2014 on woody vegetation within the Nama-Karoo and semi-arid savanna biomes of South Africa. J. Arid Environ. 133, 112–121.
- Nickless, A., Scholes, R.J., Archibald, S., 2011. A method for calculating the variance and confidence intervals for tree biomass estimates obtained from allometric equations. South African J. Sci. 107, 1–10.
- Odipo, V.O., Nickless, A., Berger, C., Baade, J., Urbazaev, M., Walther, C., Schmullius, C., 2016. Assessment of aboveground woody biomass dynamics using terrestrial laser scanner and 1-band ALOS PALSAR data in South African Savanna. Forests, 7, 294.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M., 2007. The vegan package. Community ecology package 10, 719.
- Owen-Smith, N., Cooper, S.M., 1987. Palatability of woody plants to browsing ruminants in a South African savanna. Ecology 68, 319–331.
- Palmer, A.R., Weideman, C., Finca, A., Everson, C.S., Hanan, N., Ellery, W., 2015. Modelling annual evapotranspiration in a semi-arid, African savanna: functional convergence theory, MODIS LAI and the Penman–Monteith equation. Afr. J. Range Forage Sci. 32 (1), 33–39.
- Peters, C., 1996. Ecology and Management of Non-Timber Forest Resources. World Bank Group, Washington, DC (United States). World Bank Technical Paper 322.
- Pfeiffer, M., Langan, L., Linstädter, A., Martens, C., Gaillard, C., Ruppert, J.C., Higgins, S.I., Mudongo, E.I., Scheiter, S., 2019. Grazing and aridity reduce perennial grass abundance in semi-arid rangelands – Insights from a trait-based dynamic vegetation model. Ecol. Model. 395, 11–22.
- Richter, C., Snyman, H., Smit, G., 2001. The influence of tree density on the grass layer of three semi-arid savanna types of southern Africa. Afr. J. Range Forage Sci. 18, 103–109.
- Sala, O.E., Paruelo, J.M., 1997. Ecosystem services in grasslands. Nature's services: societal dependence on natural ecosystems 237–251.
- Scholes, R., Gureja, N., Giannecchinni, M., Dovie, D., Wilson, B., Davidson, N., Piggott, K., McLoughlin, C., Van der Velde, K., Freeman, A., Bradley, S., Smart, R., Ndala, S., 2001. The Environment and Vegetation of the Flux Measurement Site Near Skukuza, 44. Kruger National Park. Koedoe, pp. 73–83.
- Scholes, R.J., Dowty, P.R., Caylor, K., Parsons, D.A.B., Frost, P.G.H., Shugart, H.H., 2002. Trends in savanna structure and composition along an aridity gradient in the Kalahari. J. Veg. Sci. 13, 419–428.
- Schweiger, A.H., Irl, S.D., Svenning, J.C., Higgins, S.I., 2020. Dynamic management needs for long-lived, sporadically recruiting plant species in human-dominated landscapes. Plants, People, Planet 2, 186–200.
- Seymour, C.L., 2009. Protégé Ziziphus mucronata (Rhamnaceae) show no negative effects of competition with the nurse tree Acacia (Leguminaceae), even as adults. J. Veg. Sci. 20, 926–934.
- Seymour, C.L., 2008. Grass, rainfall and herbivores as determinants of Acacia erioloba (Meyer) recruitment in an African savanna. Plant Ecol. 197, 131–138.
- Seymour, C.L., Huyser, O., 2008. Fire and the demography of camelthorn (*Acacia erio-loba* Meyer) in the southern Kalahari evidence for a bonfire effect? Afr. J. Ecol. 46, 594–601.
- Seymour, C.L., Joseph, G.S., Calitz, W., Henschel, J.R., Ramaswiela, T., van der Merwe, H., 2022. Mean height increase in saplings of a keystone woody savanna species over 15 years similar to that over a single season. Ecosphere 13, e4173.
- Shackleton, C., Shackleton, S., 2004. The importance of non-timber forest products in rural livelihood security and as safety nets: a review of evidence from South Africa. S. Afr. J. Sci. 100, 658–664.
- Steenkamp, C.J., Vogel, J., Fuls, A., Van Rooyen, N., Van Rooyen, M.W., 2008. Age determination of Acacia erioloba trees in the Kalahari. J. Arid Environ. 72, 302–313.
- Stevens, N., Erasmus, B.F.N., Archibald, S., Bond, W.J., 2016. Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock? Philos. Trans. R. Soc. B Biol. Sci. 371, 20150437.
- Stevens, N., Lehmann, C.E.R., Murphy, B.P., Durigan, G., 2017. Savanna woody encroachment is widespread across three continents. Glob. Chang. Biol. 23, 235–244.
- The SEOSAW protocols. https://seosaw.github.io/manuals.html. Date accessed March 2020. The SEOSAW partnership, 2020. A network to understand the changing socio-ecology of the southern African woodlands (SEOSAW): challenges, benefits, and methods. Plants People Planet ppp3.10168.
- Van der Merwe, H., Van Rooyen, N., Bezuidenhout, H., Bothma, J.D.P., Van Rooyen, M.W., 2019. Vachellia Erioloba Dynamics Over 38 Years in the Kalahari Gemsbok National Park. Koedoe, South Africa, p. 61.
- Van der Walt, P., le Riche, E.N., 1984. The influence of veld fire on an *Acacia erioloba* community in the Kalahari Gemsbok National Park. Koedoe 27, 103–106.
- Williams, C.A., Reichstein, M., Buchmann, N., Baldocchi, D., Beer, C., Schwalm, C., Wohlfahrt, G., Hasler, N., Bernhofer, C., Foken, T., Papale, D., 2012. Climate and vegetation controls on the surface water balance: synthesis of evapotranspiration measured across a global network of flux towers. Water Resour. Res. 48.
- Zimmermann, J., Higgins, S.I., Grimm, V., Hoffmann, J., Linstädter, A., 2010. Grass mortality in semi-arid savanna: the role of fire, competition and self-shading. Perspect. Plant Ecol. Evol. Syst. 12, 1–8.