

Drought tolerant forb flora of a semi-arid protected savanna in the Lowveld of South Africa

Authors

H. van Coller¹ 
 J. Klem¹ 
 F. Siebert¹ 

Affiliations

¹Unit for Environmental Sciences and Management, North-West University, Private Bag X6001, Potchefstroom 2520, South Africa.

Corresponding Author

Dr H. van Coller
 helga.vancoller@nwu.ac.za.

Dates

Submitted: 20 September 2019
 Accepted: 2 July 2020
 Published: 24 February 2021

How to cite this article:

Van Coller, H., Klem, J. & Siebert, F., 2021, 'Drought tolerant forb flora of a semi-arid protected savanna in the Lowveld of South Africa', *Bothalia* 51(1), a10. <http://dx.doi.org/10.38201/btha.abc.v51.i1.10>

Background: Increased frequency and intensity of droughts related to climate change are predicted to induce pressure on herbaceous communities. Considering that forbs contribute significantly to savanna ecosystem resilience, we investigated forb communities of a protected semi-arid savanna during an extensive drought.

Objective: We identified drought-tolerant species with their related functional traits.

Results: Drought-tolerant forb flora comprised of several plant families and species with overlapping traits, of which the ability to resprout was related to perennials, whereas succulence and prostrate growth form were typical annual forb dominance traits.

Conclusion: Results highlight the functional importance of forbs and their resilience to drought events in protected areas.

Keywords: resprouting; herbaceous communities; functional traits; resilience; climate change.

Introduction

Predicted increasing drought intensity and frequency, combined with higher average temperatures due to global climate change, are threatening biodiversity, and therefore the stability, functioning and sustainability of terrestrial ecosystems (Barros et al. 2018). Drought is a common phenomenon in semi-arid rangelands (Vetter 2009) and has been shown to cause rapid and lasting effects on vegetation dynamics and ultimately ecosystem function and services (Barros et al. 2018; Ploughé et al. 2019).

Depending on intensity, droughts can cause shifts in plant species assemblages, leading to the establishment of different plant communities (Junk et al. 2018). In herbaceous layers of semi-arid savannas, these communities are composed mainly of annual grasses and both annual and perennial forbs (O'Connor 1998; Buitewerf et al. 2011). In the savanna context, the term 'forb' is used to classify anything other than trees, shrubs and grasses, which has led to a poor functional definition of this life form. For the purpose of this study, we will define forbs as non-graminoid vascular plants with limited woody tissue and with perennating buds at or below soil surface. Drought episodes tend to favour forbs, since they possess a variety of drought-tolerant traits such as underground storage organs (Siebert et al. 2019) associated with persistent bud banks and viable seed banks (Siebert & Dreber 2019). Despite being associated with savanna land degradation and therefore perceived as being an undesirable functional group by land managers (Fynn & O'Connor 2000; Tessaema et al. 2011), forbs are important through providing ecosystem functions

(i.e. forage stability) during stressed conditions, and functional redundancy to absorb disturbances such as sustained grazing and droughts (Van Coller et al. 2018).

Forbs are an important source of nutritious forage and may constitute an important part of ungulate diets at certain times of the year (Du Toit 2003; Van Der Merwe & Marshal 2012). Moreover, forbs contribute significantly to the biodiversity of savanna and grassland systems (Buitenwerf et al. 2011; Siebert & Scogings 2015), which are functionally diverse, suggesting a stronger resilience to different environmental conditions (Turner & Knapp 1996; Van Coller et al. 2018). Forb ecology research in dry African savannas generally report on forb responses at the level of functional group rather than species level. Furthermore, variations in forb functional traits defining plant strategies for regeneration and survival in adaptation to climate extremes such as droughts, remain understudied (Siebert & Dreber 2019).

Below-average rainfall in the Central Lowveld of South Africa was recorded for two consecutive years (2015 and 2016) (Swemmer et al. 2018). Using data collected during this time, we sought to identify specific drought tolerant forb species and their respective functional traits in a semi-arid African savanna. In doing so, we aimed to enhance knowledge of the attributes that allow these forb species to persist during droughts and potential functions that they fulfil under such environmental conditions.

Materials and Methods

Forb communities were studied in the semi-arid savanna of the greater Kruger National Park (KNP). Protected areas are not exempt from natural disasters, such as drought. They therefore provide valuable natural experimental settings where spatial heterogeneity and ecological responses function under natural drivers (Pickett et al. 2003). These areas host a variety of indigenous wildlife including mixed feeders (e.g. elephants [*Loxodonta africana* (Blumenbach, 1797)]; impala [*Aepyceros melampus* (Lichtenstein, 1812)]), browsers (e.g. greater kudu [*Tragelaphus strepsiceros* (Pallas, 1766)]; bushbuck [*Tragelaphus sylvaticus* (Sparrman, 1780)]), and grazers (e.g. blue wildebeest [*Connochaetes taurinus* (Burchell, 1823)]; plains zebra [*Equus quagga* (Boddaert, 1785)]), amongst others (Van der Waal et al. 2011; Scogings et al. 2012).

Field surveys were undertaken at two sites of similar geology (i.e. granite and gneiss), but different soil nutrient statuses (i.e. nutrient-rich sodic soil versus nutrient-poor sandy soil). Floristic and functional trait data were collected from 48 plots of 1 m² (18 plots within the nutrient-rich site and 30 plots within the nutrient-poor site) during the usual rainy season (November–March) of the extensive drought of 2015/2016. In the KNP (i.e.

nutrient-rich site), total annual rainfall was 200 mm below the mean annual rainfall for the area (Van Coller et al. 2018), while at the nutrient-poor site in Timbavati Private Nature Reserve (TPNR) it was ~330 mm below the long-term average (Kaschula et al. 2005). Within each plot, forbs were identified up to species level and all individuals counted. Frequency per species was calculated with respect to all recorded species in each respective site. Frequency is considered a stable variable for the abundance of an individual species (O'Connor 2015). Frequency measures (%) were used to identify forb species most commonly observed in the study sites. Only forb species with a frequency ≥ 1 are discussed. Functional traits were assigned to forb species (Cornelissen et al. 2003; Germishuizen & Meyer 2003) based on the potential contribution to the functioning of semi-arid protected areas (i.e. palatability, life history and nitrogen-fixing ability), as well as the ability to tolerate conditions related to drought and herbivory (growth form, life history, resprouting capacity and succulence).

Results and Discussion

Herbaceous productivity is strongly affected by rainfall, and generally reveals marked deterioration in response to drought conditions (Figure 1) (Fynn & O'Connor 2000; O'Connor 2015). Despite this, frequency measures revealed a total of 31 forb species among the two study sites. A mean number of six and four forb species was recorded per plot (1 m²) in the nutrient-rich and nutrient-poor sites respectively. The number of forb species per plot recorded in the nutrient-rich site ranged from one to 17, while a lower range (0–7) of forb species were recorded for plots in the nutrient-poor site.

Plant families that comprised most of the frequent taxa during the drought included Acanthaceae and



Figure 1. Sparsely vegetated sampling sites within the KNP (A) and TPNR (B) during the drought.

Amaranthaceae in the nutrient-rich site, and Fabaceae and Boraginaceae in the nutrient-poor site (Table 1). Prevalence of the Fabaceae is in accordance with Wagner et al. (2016) who reported that nitrogen-fixing herbaceous legumes from the Fabaceae may increase in abundance after disturbances in dry savanna rangelands, and also in disturbed grasslands (Muller et al. 2021). Nitrogen-fixing ability is a trait generally associated with ecosystems with low nutrient availability (Cornelissen et al. 2003), explaining the high frequency of *Chamaecrista mimosoides* (L.) Greene in the nutrient-poor site (Table 1). Over 50% of the most frequent forbs were annuals (Table 1). Annual forbs have been reported to form a major component of soil seed banks, especially under heavy grazing (O'Connor 1991; Tessema et al. 2016), potentially enabling them to respond and establish rapidly when conditions become favourable (e.g. smaller rainfall events interrupting extensive droughts). The occurrence of bare soil caused by herbivores and drought is known to facilitate the colonisation of prostrate forb species (Burkepile et al. 2016). *Blepharis integrifolia* (L.f.) E.Mey. ex Schinz, a palatable, perennial and low-growing forb is known to form patches of continuous groundcover or 'browsing lawns' in heavily utilised sodic bottomlands (Siebert & Scogings 2015), whilst the prostrate-growing annual *Cisekia africana* (Lour.) Kuntze revealed the highest frequency in the nutrient-poor site (Table 1). Persistence of these species is therefore likely attributed to the positioning of perennating tissue at or close to the soil surface, since fewer species could have buds far above the soil surface during harsher climatic conditions such as drought (Cornelissen et al. 2003). Moreover, erect growing plant species with their perennating buds situated above the soil surface are especially susceptible to trampling, heavy grazing and exposure to extreme heat conditions, whereas prostrate-growing species are avoidant by retaining buds and leaf material close to the soil surface (Cornelissen et al. 2003). A prostrate growth form in forbs could therefore be considered an important resistance trait against drought and grazing in the protected Lowveld savannas of South Africa.

The presence of annual forb species with a pioneer character in seed banks (Tessema et al. 2016) allows for their initial colonisation of bare soil (Siebert & Dreber 2019). Therefore, some of the most frequently observed forb species during the drought (i.e. *Portulaca kermesina* N.E.Br. and *P. hereroensis* Schinz in the nutrient-rich site, and *G. africana* in the nutrient-poor site) were annuals (Table 1). Moreover, these species exhibited traits generally associated with grazing- and drought-tolerance (i.e. prostrate growth form and succulence) (Cornelissen et al. 2003). Although little is known about succulence as a drought-tolerant trait in forbs, the ability of these species to retain water in their leaves and stems during dry conditions, together with a prostrate growth form to avoid and tolerate herbivory, possibly favoured their survival when subjected to herbivore utilisation in dry, hot conditions. Annual forbs exhibiting this combination of traits therefore make up

an important component of the forb flora of semi-arid protected areas, especially during a drought.

The majority of drought-tolerant perennial forbs in this study had the ability to resprout, either through buds located at or near the soil surface, or belowground. Such a disturbance-tolerant trait is well-known for trees and shrubs, but our understanding of regeneration from buds in forbs is unknown and requires further investigation (Siebert & Dreber 2019).

Over half of the frequent forb species recorded during the drought were palatable (Table 1). This reinforces the functional importance of the forb component through their ability to provide important ecosystem functions, such as forage stability during stressed conditions, and functional redundancy enabling them to absorb disturbances such as sustained grazing and drought (Van Colle et al. 2018).

Conclusion

Despite anticipated deterioration of the herbaceous layer during droughts, forbs have the ability to withstand such disturbances through species-specific adaptions. Numerous forb species were able to persist amidst the abnormal hot and dry conditions, while providing the ecosystem with important functions and services, such as forage stability. Plant strategies for survival and regeneration during drought conditions are species- and family specific, which may vary across ecosystem types. Furthermore, drought-adaptations were also specific for life history groups, as annuals displayed strategies to survive after emergence (e.g. succulence and prostrate growth form), whilst the majority of perennial forbs had the ability to resprout from a persistent bud bank. As protected areas aim to conserve biodiversity, provide forage security for wildlife and to maintain ecosystem resilience, this study demonstrates that forbs contribute to these at plant taxonomic and functional trait levels.

Authors' contributions

HvC (North-West University) collected vegetation data from the Nkuhlu exclosures at the Kruger National Park (KNP), analyzed and reported data and wrote the manuscript, whilst JK (North-West University) collected data from Timbavati Private Nature Reserve (TPNR). FS (North-West University) was the project leader, promoter and supervisor to HvC and JK respectively, and was responsible for project design, data collection, reporting and the writing of the manuscript.

Disclaimer

The authors declare that the work presented, and views expressed in this submitted article is their own and is

Table 1: Frequent forb species in the semi-arid savanna of the Greater KNP during a drought with a summary of relevant functional traits. Trait data were derived from field guides and various Floras

Species	Family	Life history	Growth form	Palatability ^S	Resprouting capacity	Nitrogen fixator	Succulence	Frequency
Nutrient-rich site (KNP)								
<i>Blepharis integrifolia</i> (L.f.) E.Mey. ex Schinz	Acanthaceae	Perennial	Prostrate	High	Aboveground	No	No	45.8
<i>Portulaca kermesina</i> N.E.Br.	Portulacaceae	Annual	Prostrate	High	–	No	Leaves and stems	5.8
<i>Ruellia cordata</i> Thunb.	Acanthaceae	Perennial	Erect leafy	High	Belowground	No	No	4.4
<i>Phyllanthus incurvus</i> Thunb.	Euphorbiaceae	Perennial	Erect leafy	Moderate	Aboveground	No	No	4.0
<i>Bidens bipinnata</i> L.*	Asteraceae	Annual	Erect leafy	Moderate	–	No	No	2.8
<i>Waltheria indica</i> L.*	Sterculiaceae	Perennial	Erect leafy	Low	Aboveground	No	No	2.6
<i>Portulaca hereroensis</i> Schinz	Portulacaceae	Annual	Prostrate	Low	–	No	Leaves and stems	2.5
<i>Acalypha indica</i> L.	Euphorbiaceae	Annual	Erect leafy	Moderate	–	No	No	2.1
<i>Commelinina benghalensis</i> L.	Commelinaceae	Annual	Erect leafy	High	Above and belowground	No	No	2.1
<i>Hibiscus micranthus</i> L.f.	Malvaceae	Perennial	Erect leafy	High	Belowground	No	No	2.1
<i>Kyphocarpa angustifolia</i> (Mod.) Lopr.	Amaranthaceae	Annual	Erect leafy	High	–	No	No	2.1
<i>Ocimum americanum</i> L.	Lamiaceae	Perennial	Erect leafy	Low	Aboveground	No	No	2.1
<i>Evolvulus alsinoides</i> (L.) L.	Convolvulaceae	Annual	Erect leafy	Moderate	–	No	No	1.4
<i>Gomphrena celosioides</i> Mart.*	Amaranthaceae	Perennial	Prostrate	Moderate	Aboveground	No	No	1.4
<i>Justicia flava</i> (Vahl) Vahl	Acanthaceae	Perennial	Erect leafy	Moderate	–	No	No	1.4
<i>Achyranthes aspera</i> L.*	Amaranthaceae	Perennial	Erect leafy	High	–	No	No	1.2
<i>Indigofera filipes</i> Benth. ex Harv.	Fabaceae	Annual	Erect leafy	Moderate	–	Yes	No	1.2
Nutrient-poor site (TPNR)								
<i>Gisekiaria africana</i> (Lour.) Kuntze	Gisekiaceae	Annual	Prostrate	Low	–	No	Leaves and stems	35.3
<i>Chamaecrista mimosoides</i> (L.) Greene	Fabaceae	Annual	Erect leafy	Moderate	–	Yes	No	11.2
<i>Heliotropium strigosum</i> Willd.	Boraginaceae	Annual	Erect leafy	Low	–	No	No	6.0
<i>Commelinina benghalensis</i> L.	Commelinaceae	Annual	Erect leafy	High	Above and belowground	No	No	4.8
<i>Leucas sexdentata</i> Skan	Lamiaceae	Annual	Erect leafy	Low	–	No	No	4.4
<i>Phyllanthus maderaspatensis</i> L.	Euphorbiaceae	Perennial	Erect leafy	Moderate	Aboveground	No	No	4.1
<i>Chamaecrista absus</i> (L.) Irwin & Barneby	Fabaceae	Annual	Erect leafy	Low	–	Yes	No	2.3
<i>Phyllanthus parvulus</i> Sond.	Euphorbiaceae	Perennial	Erect leafy	Moderate	–	No	No	2.3
<i>Schkuhria pinnata</i> (Lam.) Cabrera*	Asteraceae	Annual	Erect leafy	Low	–	No	No	1.8
<i>Sida ovata</i> Forsk.	Malvaceae	Annual	Erect leafy	Low	Belowground	No	No	1.8
<i>Bidens bipinnata</i> L.*	Asteraceae	Annual	Erect leafy	Moderate	–	No	No	1.6
<i>Heliotropium ovalifolium</i> Forssk.	Boraginaceae	Annual	Erect leafy	Low	Belowground	No	No	1.6
<i>Heliotropium ciliatum</i> Kaplan	Boraginaceae	Perennial	Erect leafy	Low	Belowground	No	No	1.4
<i>Tephrosia longipes</i> Meisn.	Fabaceae	Annual	Erect leafy	Low	Aboveground	No	No	1.4

^S This categorical trait is based on an adapted version of Walker's Palatability Index (Siebert & Scogings 2015), to detect browsing signs from smaller ungulates. Species preference of larger herbivores (e.g. elephant) remains poorly known as they often uproot the entire plant. For the purpose of this trait data, a forb was considered palatable if it showed any signs of browsing, irrespective of the type of large herbivore; Alien species are indicated with asterisk (*).

not an official position of the institution or funder. The authors furthermore declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

References

Barros, C., Thuiller, W. & Münkemüller, T., 2018, 'Drought effects on the stability of forest-grassland ecotones under gradual climate change', *PLoS ONE*, 13(10), 1–18. <https://doi.org/10.1371/journal.pone.0206138>.

Buitenwerf, R., Swemmer, A.M. & Peel, M.J.S., 2011, 'Long-term dynamics of herbaceous vegetation structure and composition in two African savanna reserves', *Journal of Applied Ecology*, 48(1), 238–246. <https://doi.org/10.1111/j.1365-2664.2010.01895.x>.

Burkepile, D.E., Thompson, D.I., Fynn, R.W.S., Koerner, S.E., Eby, S., Govender, N., Hagenah, N., Lemoine, N.P., Matchett, K.J., Wilcox, K.R., Collins, S.L., Kirkman, K.P., Knapp, A.K. & Smith, M.D., 2016, 'Fire frequency drives habitat selection by a diverse herbivore guild impacting top-down control of plant communities in an African savanna', *Oikos*, 125, 1636–1646. <https://doi.org/10.1111/oik.02987>.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pauses, J.G. & Poorter, H., 2003, 'A handbook of protocols for standardised and easy measurement of plant functional traits worldwide', *Australian Journal of Botany*, 51(4), 335. <https://doi.org/10.1071/bt02124>.

Du Toit, J.T., 2003, 'Large herbivores and Savanna heterogeneity', in du Toit, J.T., Biggs, H.C. & Rogers, K.H. (eds.), *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, pp. 292–309, Washington, DC: Island Press.

Fynn, R.W.S. & O'Connor, T.G., 2000, 'Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa', *Journal of Applied Ecology*, 37(3), 491–507. <https://doi.org/10.1046/j.1365-2664.2000.00513.x>.

Germishuizen, G. & Meyer, N.L. (eds.), 2003, 'Plants of southern Africa: an annotated checklist', *Strelitzia* 14, Pretoria: National Botanical Institute.

Junk, W.J., Piedade, M.T.F., Cunha, C.N. da, Wittmann, F. & Schöngart, J., 2018, 'Macrohabitat studies in large Brazilian floodplains to support sustainable development in the face of climate change', *Ecohydrology and Hydrobiology*, 18(4), 334–344. <https://doi.org/10.1016/j.ecohyd.2018.11.007>.

Kaschula, S.A., Twine, W.E., & Scholes, M.C., 2005, 'Copice harvesting of fuelwood species on a South African common: Utilizing scientific and indigenous knowledge in Community Based Natural Resource Management', *Human Ecology*, 33, 387–418. <https://doi.org/10.1007/s10745-005-4144-7>.

Muller, M., Siebert, S.J., Ntloko, B.R. & Siebert, F., 2021, 'A floristic assessment of grassland diversity loss in South Africa', *Bothalia* 51(1): 147–155 (hardcopy); 1–9 (online) [this issue].

O'Connor, T.G., 1991, 'Influence of rainfall and grazing on the compositional change of the herbaceous layer in the savanna regions of southern Africa', *Journal of the Grassland Society of southern Africa*, 8, 103–109. <https://doi.org/10.1080/02566702.1991.9648273>.

O'Connor, T.G., 1998, 'Impact of sustained drought on a semi-arid *Colophospermum mopane*', *African Journal of Range and Forage Science*, 15(3), 83–91. <https://doi.org/10.1080/10220119.1998.9647948>.

O'Connor, T.G., 2015, 'Long-term response of an herbaceous sward to reduced grazing pressure and rainfall variability in a semi-arid South African savanna', *African Journal of Range and Forage Science*, 32(4), 261–270. <https://doi.org/10.2989/10220119.2015.1015052>.

Pickett, S.T.A., Cadenasso, M.L. & Benning, T.L., 2003, 'Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales', in du Toit, J.T., Biggs, H.C. & Rogers, K.H. (eds.), *The Kruger Experience: Ecology and management of savanna heterogeneity*, pp. 22–40, Island Press, Washington, DC.

Plough, L.W., Jacobs, E.M., Frank, G.S., Greenler, S.M., Smith, M.D., & Dukes, J.S., 2019, 'Community Response to Extreme Drought (CRED): a framework for drought-induced shifts in plant-plant interactions', *New Phytologist*, 222, 52–69. <https://doi.org/10.1111/nph.15595>

Scogings, P.F., Johansson, T., Hjältén, J. & Kruger, J., 2012, 'Responses of woody vegetation to exclusion of large herbivores in semi-arid savannas', *Austral Ecology*, 37(1), 56–66. <https://doi.org/10.1111/j.1442-9993.2011.02249>.

Scogings, P.F., Hattas, D., Skarpe, C., Hjältén, J., Dziba, L., Zobollo, A., & Rooke, T., 2015, 'Seasonal variations in nutrients and secondary metabolites in semi-arid savannas depend on year and species', *Journal of Arid Environments*, 114, 54–61. <https://doi.org/10.1016/j.jaridenv.2014.11.003>.

Siebert, F. & Scogings, P.F., 2015, 'Browsing intensity of herbaceous forbs across a semi-arid savanna catena sequence', *South African Journal of Botany*, 100, 69–74. <https://doi.org/10.1016/j.sajb.2015.05.007>.

Siebert, F. & Dreber, N., 2019, 'Forb ecology research in dry African savannas: Knowledge, gaps, and future perspectives', *Ecology and Evolution*, 9, 7875–7891. <https://doi.org/10.1002/ece3.5307>.

Siebert, F., Bombo, A.B., Archibald, S., Greve, M., & Fidelis, A., 2019, 'Introducing bud bank and below-ground plant organ research to South Africa: Report on a workshop and the way forward', *South African Journal of Science*, 115(11/12), Art.#6803. <https://doi.org/10.17159/sajs.2019/6803>.

Swemmer, A.M., Bond, W.J., Donaldson, J., Hempson, G.P., Malherbe, J. & Smit, I., 2018, 'The ecology of drought

– a workshop report', *South African Journal of Science*, 114(9/10), 9–11. <https://doi.org/10.17159/sajs.2018/5098>.

Tessema, Z.K., de Boer, W.F., Baars, R.M.T. & Prins, H.H.T., 2011, 'Changes in soil nutrients, vegetation structure and herbaceous biomass in response to grazing in a semi-arid savanna of Ethiopia', *Journal of Arid Environments*, 75(7), 662–670. <https://doi.org/10.1016/j.jaridenv.2011.02.004>.

Tessema, Z.K., de Boer, W.F. and Prins, H.H.T., 2016, 'Changes in grass plant populations and temporal soil seed bank dynamics in a semi-arid African savanna: Implications for restoration', *Journal of Environmental Management*, 182, 166–175. <https://doi.org/10.1016/j.jenvman.2016.07.057>

Turner, A.C.L. & Knapp, A.K., 2008, 'Responses of a C4 Grass and three C3 forbs to variation in nitrogen and light in Tall-grass Prairie', *Ecological Society of America*, 77(6), 1738–1749. <http://www.jstor.org/stable/2265779>.

Van Coller, H., Siebert, F., Scogings, P.F., & Ellis, S., 2018, 'Herbaceous responses to herbivory, fire and rainfall variability differ between grasses and forbs', *South African Journal of Botany*, 119, 94–103. <https://doi.org/10.1016/j.sajb.2018.08.024>.

Van Der Merwe, J. & Marshal, J.P., 2012, 'Hierarchical resource selection by impala in a savanna environment', *Austral Ecology*, 37(3), 401–412. <https://doi.org/10.1111/j.1442-9993.2011.02297.x>.

Van der Waal, C., Kool, A., Meijer, S.S., Kohi, E., Heitkönig, I.M.A., de Beer, W.F., van Langevelde, F., Grant, R.C., Peel, M.J.D., Slowtow, R., de Knegt, H.J., Prins, H.H.T., & de Kroon, H., 2011, 'Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation', *Oecologia*, 165(4), 1095–1107. <https://doi.org/10.1007/s00442-010-1899-3>.

Vetter, S., 2009, 'Drought, change and resilience in South Africa's arid and semi-arid rangelands.', *South African Journal of Science*, 105(1/2), 29–33. <https://doi.org/10.1590/s0038-23532009000100017>.

Wagner, T. C., Hane, S., Joubert, D.F. & Fischer, C., 2016, 'Herbaceous legume encroachment reduces grass productivity and density in arid rangelands', *PLoS ONE*, 11(11), 1–13. <https://doi.org/10.1371/journal.pone.0166743>.