

Key determinants of long-term compositional variation of the herbaceous layer in a semi-arid African savanna: Rainfall, soil type, and plant species functional types

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Management of the grazing resource in semi-arid savanna is dependent on inter-annual variation in available moisture, which is determined by rainfall, soil type and woody biomass. Grazing and fire may further influence trends. Understanding the effect of rainfall variability requires study over an 18-year quasi-cycle of rainfall with frequent measurement, a constraint which few southern African studies have met. The herbaceous layer and woody vegetation on deep (> 0.6 m) well-drained sands, moderately deep (0.3–0.6 m) well-drained sands, moderately deep poorly drained clays, and shallow (< 0.3 m) rocky moderately drained sandy loams in the deproclaimed Vaalbos National Park, South Africa, were monitored from 1993 to 2015. Woody density and structure differed conspicuously across soil types, but there were no trends noticed over time for the park or for any individual soil type. There was also no change in the number of woody species or frequency distribution over this survey period. Different functional groups responded differently to rainfall or to soil water storage capacity of the soil profile. Palatable and unpalatable perennial grasses both responded to rainfall of the current and previous season but in different ways. The decline of palatable perennial grasses in response to increasing rainfall was influenced in part by use of relative rather than absolute abundance. This indicates that in wet years annual grasses proliferated between perennial grass tufts and were therefore measured as closest to point of sampling. This influence of annual grasses obscures whether perennial grasses changed in absolute terms. Constraints around a lack of personnel, time and budget often determine the type of monitoring that it is feasible to conduct – a concern and probably the reason why so many monitoring datasets and results are not published.

Keywords: long-term vegetation monitoring, statistics, semi-arid region, different soil types, herbaceous layer

Introduction

Savanna covers about 40% of Africa's land surface (Cole 1986) and is used primarily for support of livestock or wildlife based on indigenous vegetation (Barnes 1982). Dominant plant growth forms of this biome include woody plants (trees, shrubs), dwarf shrubs, graminoids, non-graminoid monocotyledons and herbaceous dicotyledons (Mucina & Rutherford 2006), but herbaceous biomass is dominated by grasses (Zietsman & Bezuidenhout 1999; Parr *et al.* 2014). As a consequence, savanna functioning is determined largely by the relation between trees and grasses (Sankaran *et al.* 2004) with, to date, the role of a conspicuous richness of forbs largely unrecognised (Clegg & O'Connor 2017). Effective use and management of this vegetation resource therefore requires an improved understanding of the influences which determine the composition, structure, and dynamics of each.

The primary determinants of savanna organisation are water and nutrient availability (Frost *et al.* 1986; Wiegand *et al.* 1998). Water availability is a function of rainfall and water storage in soil profile determined by its depth and texture (Ritchie 1981). Nutrient availability is also determined by soil texture, such that the dual effects of water and nutrient availability are confounded and cannot be separated (Foth 1990). Secondary determinants of savanna vegetation are fire and herbivory (Smit *et al.* 2013), both grazing (Tainton 1999) and browsing (Belsky 1984; Augustine & McNaughton 2004; Moe *et al.* 2009). Fire can potentially transform savanna structure because of its effect on trees and shrubs (Van der Walt & Le Riche 1984; Seymour & Huyser 2008) but can also transform herbaceous composition when acting in combination with heavy grazing (O'Connor 1985). Identification of an effect of an individual determinant therefore requires that the impact of the other determinants is taken into account.

These four determinants (water, nutrient availability, fire and herbivory) provide a minimum template for improving prediction of savanna dynamics. Foremost for southern African savannas is the influence of inter-annual rainfall variation, which is inversely related to mean annual rainfall for southern Africa (Tyson & Preston-Whyte 2000). Thus semi-arid savannas are more variable, and more prone to drought, than their mesic counterparts. Drought impacts are more severe on high clay-content textured soils but are buffered by sandy soils (Dye & Spear 1992). Rainfall of the preceding season may influence vegetation growth during the following season through carry-over effects (O'Connor *et al.* 2001). Inter-annual variability may also involve shifts in the seasonal distribution of rainfall (Du Toit & O'Connor 2014). Vegetation changes in response to grazing and fire management may depend critically on rainfall patterns over years (Westoby *et al.* 1989). Plant communities may change dramatically when certain factors combine, for example transformation of the herbaceous layer by heavy grazing continuing through an extended drought (Illius & O'Connor 1999). Consequences of such a combination of factors may persist for decades, as witnessed for bush encroachment and densification in southern Africa following the 1960s drought or the withdrawal of fire during high rainfall years suitable for woody recruitment (O'Connor *et al.* 2014). Such increases in woody cover further affect the herbaceous sward (Dye & Spear 1982; Belsky *et al.* 1989; Smit 2004).

The herbaceous layer exhibits a wide range of life history types including long-lived perennials, biennials, and annuals, whose pattern of dynamics is intrinsically different (Harper 1977). Success of annual species in semi-arid southern African savanna is considered to depend on receiving adequate rainfall during the early part of the rainfall season so that there is sufficient time to attain reproductive status; seeds may therefore be cued not to germinate in the late rainy season (Veenendaal *et al.* 1996a, b). Species are also intrinsically different in their tolerance or response to specific environmental conditions. A species growing near its climatic optimum would not be expected to respond to inter-annual rainfall variability in the same manner as one growing near the margin of its distribution. Herbaceous species and functional groups, including dwarf shrubs, differ in their response to drought (O'Connor 2015) and to variation in intra-seasonal pattern of rainfall (O'Connor & Roux 1995; Swemmer *et al.* 2007). Herbaceous species respond differently to grazing, exemplified by their increaser-decreaser classification and to fire (Tainton 1999). In summary, individualistic species responses should be expected to the many constellations of environmental influences which may arise.

This paper addresses the influence of inter-annual variability in available moisture, as determined by rainfall modified by soil types, on the variability of functional groups and dominant species of the herbaceous layer of a semi-arid savanna. The deproclaimed Vaalbos National

Park (hereafter Vaalbos), South Africa, contains contrasting soil types (Bezuidenhout 1994, 1995) of which the associated vegetation was monitored for a period (1993–2015) equivalent to the quasi-18-year cycle characteristic of summer rainfall regions in southern Africa (Tyson & Preston-Whyte 2000). In order to provide a clear context for assessing changes, the following was our main aim: (i) to describe the pattern of rainfall; (ii) to determine whether grazing, browsing and fire could be discounted as important agents of change; and (iii) to determine whether the woody component had changed or its effect could be discounted. (iv) To also determine plant functional types and how the dominant species responded to annual variation in plant available moisture as determined by annual rainfall and soil type, seasonal concentration of rainfall (early versus late), and soil properties (soil depth and texture). Arising from this, the relative measures of plant abundance (which offers a reliable means of assessing compositional change over time), was also assessed.

Vegetation monitoring is one of the mainstays for biodiversity assessment for SANParks and it is being underpinned by SANParks' Strategic Adaptive Management (SAM) approach (McGeoch *et al.* 2011). It should be coupled to strongly goal-orientated park objectives which are linked to science, monitoring and management (Biggs & Rogers 2003). It is important that lessons learned from the vegetation monitoring in Vaalbos should guide a vegetation monitoring programme for the newly proclaimed Mokala National Park.

Study area

Vaalbos was situated in the Northern Cape, South Africa (28°25–40'S; 24°12–46'E) (Figure 1). Vaalbos was proclaimed in 1986 but deproclaimed in 2002 following a successful land claim lodged in 1998 (Bezuidenhout *et al.* 2016). The climate is semi-arid, with annual (July to June) rainfall for the period 1993 to 2015 averaging 396 mm per annum (range 215 to 601 mm) (Figure 2). Most rain falls during summer as convective events. Summers are hot with daily maxima > 35 °C during December and January, and winters are mild but with regular frost occurrence during the peak three months (May–July) (Land Type Survey Staff 2012).

Vaalbos is a flat to gently undulating landscape ranging in altitude from 1 050 to 1 187 m and drained by local ephemeral tributaries of the Vaal River. Topography includes crests, midslopes, plains, floodplains, pans and riverbanks. Surface geology of Vaalbos is diverse including outcrops of andesitic lavas occurring mainly as koppies, low quartzite ridges, aeolian sands sometimes with surface calcrete, alluvial gravels, and Dwyka tillite (Spaggiari 1993; Bezuidenhout 2009). Mining of diamond deposits within gravel-filled palaeo-watercourses of the Vaal River during the 1920s produced heaps of disturbed gravel that have persisted (Bezuidenhout 1994).

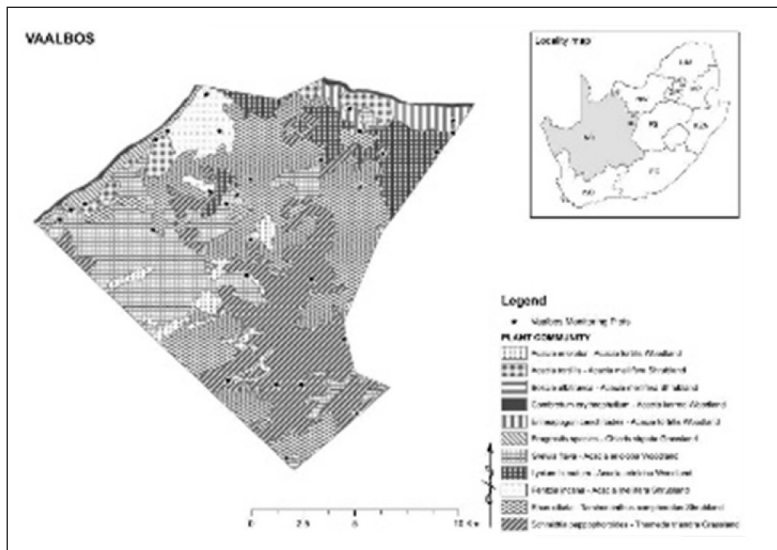


FIGURE 1: Plant communities of Vaalbos, as well as the locality of monitoring plots and locality of Vaalbos in South Africa

The area was classified by Acocks (1988) as Kalahari Thornveld invaded by Karoo (Veld Type 17), with a small section of False Orange River Broken Veld (Veld Type 40) along the banks of the Vaal River. Mucina and Rutherford (2006) mapped Kimberley Thornveld (SVk4) and Schmidtsdrif Thornveld (SVk6) of the Savanna Biome,

and Highveld Salt Pans (AZi10) as part of the Inland Azonal Vegetation. Bezuidenhout (1994) described 11 major plant communities that are closely related to specific habitat (Table 1). These 11 plant communities can be summarised as four main soil landscapes each supporting a variety of different plant communities: (i) deep (> 0.6 m) loamy sands (Hutton and Clovelly soil forms); (ii) moderate (0.3–0.6 m) deep loamy sands (Hutton and Clovelly soil forms); (iii) shallow (< 0.3 m) stony sandy clay (Mispah, Prieska, Kimberley soil forms); and (iv) moderately deep (0.3–0.6 m), silty clay loam (Valsrivier and Swartland soil forms) (Soil Classification Working Group 1991; Bezuidenhout 1994; Land Type Survey Staff 2012). Common grasses of loamy sand soils were *Schmidtia pappophoroides*, *Themeda triandra*, *Aristida stipitata*, *Aristida congesta*, *Eragrostis lehmanniana*, *Stipagrostis uniplumis*, *Pogonarthria squarrosa* and *Eragrostis pallens*. Characteristic species of silty clay soil were *Chloris virgata*, *Eragrostis bicolor*, *Eragrostis obtusa*, *Tragus berteronianus*, *Aristida adscensionis* and *Panicum coloratum*. Plant nomenclature follows Klopper *et al.* (2006), with the exception of the revised genus *Acacia*, which follows Kyalangalilwa *et al.* (2013).

TABLE 1: Summary of the plant communities of the former Vaalbos National Park (from Bezuidenhout 1994), and of the sampling intensity accorded each

Plant community	Habitat	n woody	n grass
<i>Schmidtia pappophoroides</i> - <i>Themeda triandra</i> grassland	Deep (> 1.2 m) to moderately deep (0.3–0.8 m), well-drained loamy sand of the midslope plain	0	5
<i>Grewia flava</i> - <i>Acacia erioloba</i> open woodland	Deep (> 1.2 m) well-drained red loamy sand of the midslope plain	2	2
<i>Lycium hirsutum</i> - <i>Acacia erioloba</i> open woodland	Deep (> 1.2 m) well-drained yellow loamy sand of the midslope plain	2	2
<i>Rhus ciliata</i> - <i>Tarchonanthus camphoratus</i> open shrubland	Moderately deep (0.3–0.8 m) loamy sand of the midslope plain	5	2
<i>Acacia erioloba</i> - <i>Acacia tortilis</i> open woodland	Ancient gravel-filled water courses: shallow, stony, sandy soil of the midslope plain	1	0
<i>Boscia albitrunca</i> - <i>Acacia mellifera</i> shrubland	Isolated rocky outcrops	0	0
<i>Acacia tortilis</i> - <i>Acacia mellifera</i> closed shrubland	Shallow (< 0.3 m) stony, sandy soil with large surface rocks of the midslope plain	2	0
<i>Enneapogon cenchroides</i> - <i>Acacia tortilis</i> open woodland	Recently deposited Vaal River gravel: shallow, stony and sandy; of the midslope plain	2	0
<i>Pentzia incana</i> - <i>Acacia mellifera</i> closed shrubland	Shallow (< 0.3 m) stony sandy soil (stony surface)	2	0
<i>Eragrostis species</i> - <i>Chloris virgata</i> open grassland	Moderately deep (0.3–0.8 m) silty clay soil of the floodplain	0	3
<i>Combretum erythrophyllum</i> - <i>Acacia karroo</i> woodland	Deep (> 1.2 m) silty clay loam (alluvial) soil on the banks of the Vaal River	0	0

Methods

Field monitoring

Vegetation monitoring was initiated in April 1993. The park was stratified and representative plots were selected based on plant communities (Table 1 and Figure 1). For each plot, soil depth was determined by augering and amount of clay was estimated using a finger test (Foth 1990). Herbaceous composition of five plant communities was sampled, each with three or more plots (Ferreira *et al.* 2013) to provide a total of 27 plots (Table 1 and Figure 1). A site was sampled along a 100 m permanently marked (beginning and end) transect. Herbaceous layer was sampled using a wheel-point apparatus (Tidmarsh & Havenga 1955) on twelve occasions between 1993 and 2015 (1993–1998, 2001, 2003, 2011, 2012, 2013 and 2015) although not every plot was done on each occasion. Unfortunately the land claim and the deproclamation of Vaalbos and the move of SANParks to Mokala National Park resulted in the end of SANParks formal monitoring in Vaalbos, resulting in the gap between survey dates (Bezuidenhout *et al.* 2016). Fortunately the Arid SAEON (South African Environmental Observations Network) Node was established in Kimberley and was interested to continue with the monitoring of the vegetation of the deproclaimed Vaalbos. The wheel point had two marked spokes per wheel (one per half rotation), which provided a total of 200 points per 100 m transect. Hardy & Walker (1991) suggested that 200 points should be sampled for monitoring. At each point the nearest plant species individual was recorded. If the nearest plant was a forb then the nearest grass species was also recorded. The frequency of each species was expressed as a percentage of the total number of points per sample site.

Woody vegetation of six plant communities was sampled on 16 plots, seven of which were not sampled for herbaceous composition (Table 1), using a belt transect (100 m long) in 1993, 2011 and 2015. Sampling was based on contiguous 2 m (width) by 5 m (length) sub-quadrats, within which each woody individual was recorded for species identity and height class (< 0.5; 0.5–1.0; 1.0–1.5; 1.5–2.0; 2.0–3.0; 3.0–4.0; > 4.0 m) (Mueller-Dombois & Ellenberg 1974).

Potential drivers of possible vegetation changes

Other than firebreaks, management mostly sought to extinguish natural or human-induced fires as soon as they were observed. The only fires recorded were a portion of sandy Grassland burnt in 1991, an accidental fire affecting the *Lycium hirsutum*-*Acacia erioloba* open woodland (deep, loamy sands) during the summer of 2002, and one during the winter of 2012. These fires had relatively minimal impact on the herbaceous layer in this study.

An aerial census of wildlife populations was undertaken 12 times between 1993 and 2006. Species recorded in a census were the bulk grazers white rhinoceros (*Ceratotherium simum*), buffalo (*Syncerus cafer*), zebra (*Equus burchelli*)

and roan (*Hippotragus equinus*), the grazers wildebeest (*Connochaetus gnu* / *C. taurinus*), hartebeest (*Alcelaphus caama*), gemsbok (*Oryx gazella*), tsessebe (*Damaliscus lunatus*) and warthog (*Phacochoerus aethiopicus*), the mixed feeders eland (*Taurotragus oryx*), springbok (*Antidorcas marsupialis*) and ostrich (*Struthio camelis*), and the browsers black rhinoceros (*Diceros bicornis*), giraffe (*Giraffa camelopardalis*), kudu (*Tagelaphus strepsiceros*), steenbok (*Raphicerus campestris*) and grey duiker (*Sylvicapra grimmia*) (nomenclature of mammals follows Skinner and Chimimba (2005)). Counts were not maintained after the national park was deproclaimed. Counts were converted to a stocking rate measure of livestock units (LSU) using the GRAZE model (Brown 1997). A rate of 0.06 LSU ha⁻¹ was considered appropriate for Vaalbos (Bancroft *et al.* 1998), which is lower than the rate of 0.08 LSU ha⁻¹ recommended for commercial ranching (Department of Agriculture, Forestry and Fisheries 2017).

Statistical analysis

Woody vegetation. For analysis of woody vegetation, transects were grouped according to three soil types, namely (i) deep (> 0.6 m), loamy sand, (ii) shallow (< 0.3 m), rocky soil, and (iii) moderately deep (0.3–0.6 m), silt-clay soil. In order to test for change in woody abundance, a repeated measures analysis of variance was undertaken of woody density for three soil types and three sampling occasions. The number of woody species was tested in a similar manner. It was also tested whether there had been a change in density, by soil type and height class, between 1993 and 2015. A Komolgorov-Smirnov test (Sokal & Rohlf 1981) was used to examine if height structure had changed between 1993 and 2015, using a pooled sample of all plots.

Herbaceous vegetation. Trends in herbaceous vegetation were analysed using functional groups and dominant species of each group. Functional groups were defined in terms of growth form, life history and herbivory. The eight groups defined were palatable or unpalatable perennial grasses, palatable or unpalatable annual grasses, dwarf shrubs, annual or perennial herbaceous dicotyledons (forbs) and geophytes. The sampled species of each functional group are listed in Appendix 1. The sample size of geophytes and annual forbs was insufficient for analysis. Percentage data were arcsine transformed before analysis. The number of zero values determined the manner in which a data set was analysed. In cases of few zero values the full data set was analysed using a linear mixed effects model. This was possible for six functional groups and three individual species. For the remaining groups and species, a logistic model was applied to a binary response (1 if abundance > 0; 0 for 0).

A linear mixed effects model was used to assess whether variation in abundance over time of a functional group or species was influenced by rainfall of the current season as modified by potential storage in a soil profile (product of profile depth and percent clay), rainfall of the previous season, and soil fertility (indexed by soil clay). The current

season, set as July to June inclusive of April, coincided with the time of sampling toward the end of the growing season. The variables included were therefore soil clay, soil depth, and a product of clay by depth. An effect of soil water storage would be evident from a significant interaction between rainfall and the depth-by-clay product variable. If rainfall of the current season had an effect, then it was examined if this effect resulted primarily from rainfall received during the early (July to December) or late (February to April) season. For example, annual grasses are expected to respond to early season rainfall (Veenendaal *et al.* 1996a, b). Year was included in order to assess if there was a temporal trend unrelated to rainfall. Plot was included as a random effect. An effect of each individual variable was assessed based on the effect of its deletion from a complete null model. Analyses were conducted using R (R Development Core Team 2015).

Results

Rainfall and herbivory

Over the monitoring period between 1993/94 and 2014/15, mean annual rainfall was 396 mm, nine years experienced above- and nine below-average rainfall, while four years were close to average (Figure 2). A regression of annual rainfall against year showed no directional trend. Total annual rainfall was positively related to the amount of rainfall falling between July and December ($r = 0.77$; $df = 21$; $P < 0.01$) but not to the amount received between February and April ($r = 0.33$; $df = 21$; $P > 0.05$), or to the amount falling during the preceding season ($r = 0.15$; $df = 21$; $P > 0.05$). Wetter years were therefore proportionately wetter during the early half of the season.

Stocking rate varied between 0.05 and 0.08 LSU ha⁻¹ from 1993 to 2000, whereafter it almost doubled by 2004 before declining sharply by 2006 following destocking (Figure 3). Average contribution of bulk feeders, grazers, mixed feeders and browsers was 14, 53, 22 and 10 percent respectively, over this period. Medium-sized grazers therefore comprised the bulk of animal biomass. Although no censuses were undertaken after 2006, no increase in numbers was observed on the ground. It is concluded that stocking rate exceeded recommended

norms for only three of 23 years. Stocking rate is therefore considered unlikely to have had a meaningful influence on vegetation change over this period.

Woody vegetation

Woody density differed conspicuously across soil types, but there was no trend in woody density over time for the park as a whole (Year not significant) or for any individual soil type (Year-Soil type interaction not significant) (Table 2). There was also no change ($P > 0.1$) in the number of woody species over this time period. There was no change ($P > 0.1$) in the frequency distribution across height classes between 1993 and 2015. Woody vegetation structure was therefore stable over the monitoring period and should not have induced change in herbaceous vegetation.

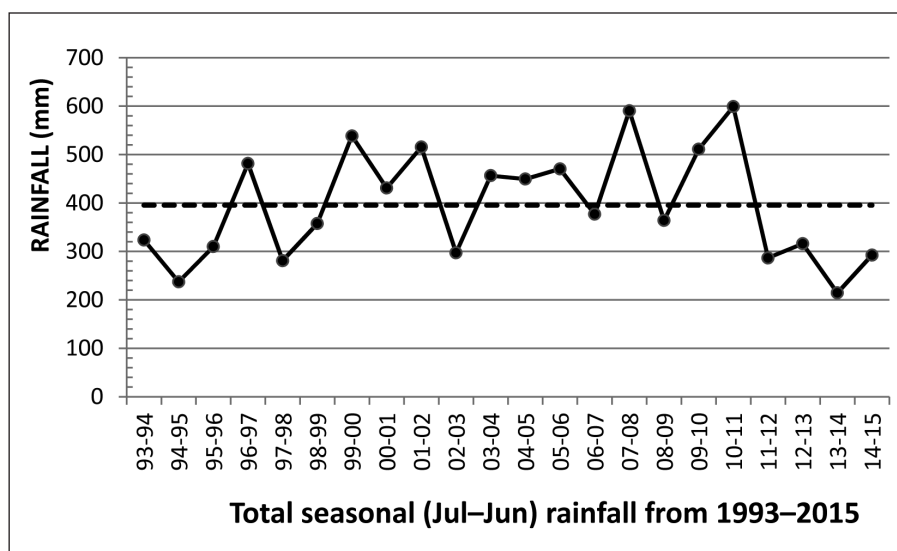


FIGURE 2: Annual (July–June inclusive) rainfall recorded between 1993 and 2015 first at Vaalbos (28°27'08.29"S 24°19'29.25"E) and then from 2006 at Rooipoort (28°38'15.31"S 24°16'49.92"E)

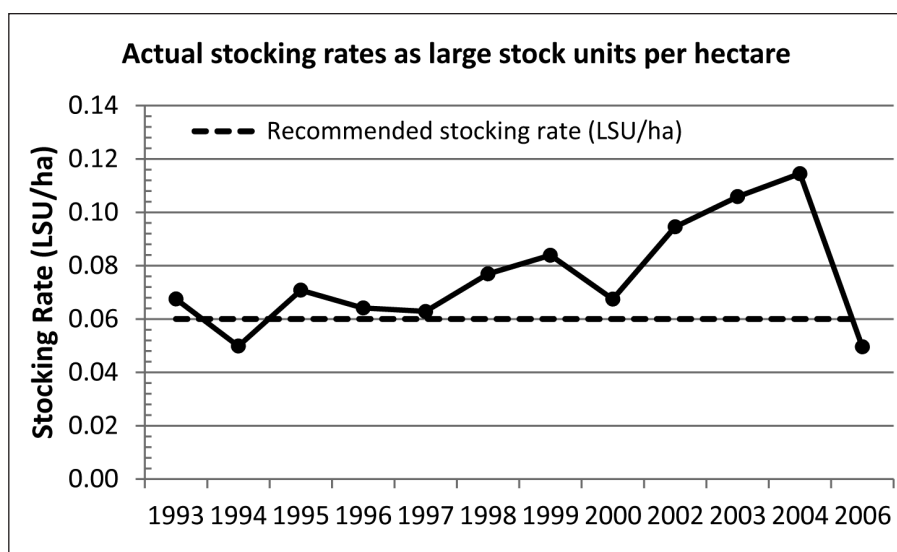


FIGURE 3: Stocking rate (LSU ha⁻¹) of the Vaalbos National Park between 1993 and 2006

TABLE 2: Summary of a repeated measures analysis of variance of woody density for the years 1993 and 2015

Model term	SS	df	MS	F	P
Intercept	161945	1	161945	42.32	0.0001
Soil type	40152	2	20076	5.25	0.0277
Error	38269	10	3827		
Year	258	2	129	0.39	0.6842
Year by soil type	135	4	34	0.10	0.9807
Error	6664	20	333		

Herbaceous vegetation

Different functional groups responded differently to rainfall or to soil water storage capacity of the soil profile

(Table 3). Palatable and unpalatable perennial grasses both responded to rainfall of the current and previous season but in different ways (Figures 4 and 5). Unexpectedly, both palatable (Figure 4a) and unpalatable (marginally) (Figure 5a) perennial grasses declined with increasing total rainfall, but palatable perennial grasses decreased (Figure 4b) whereas unpalatable perennial grasses increased (Figure 5b) in response to increased rainfall of the previous year. Unpalatable perennial grasses increased with increasing July to December rainfall, promoted further by soil water storage capacity (interaction term; Table 3), whereas palatable perennial grasses showed neither of these two responses.

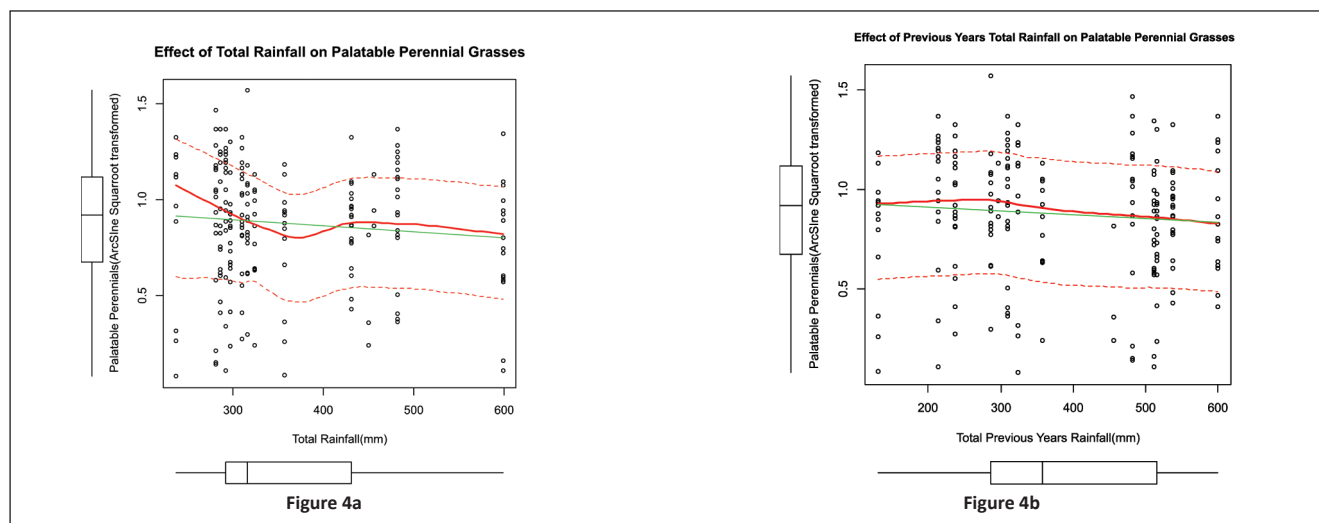


FIGURE 4: Palatable perennial grasses vs. (a) total rainfall (b) previous season rainfall

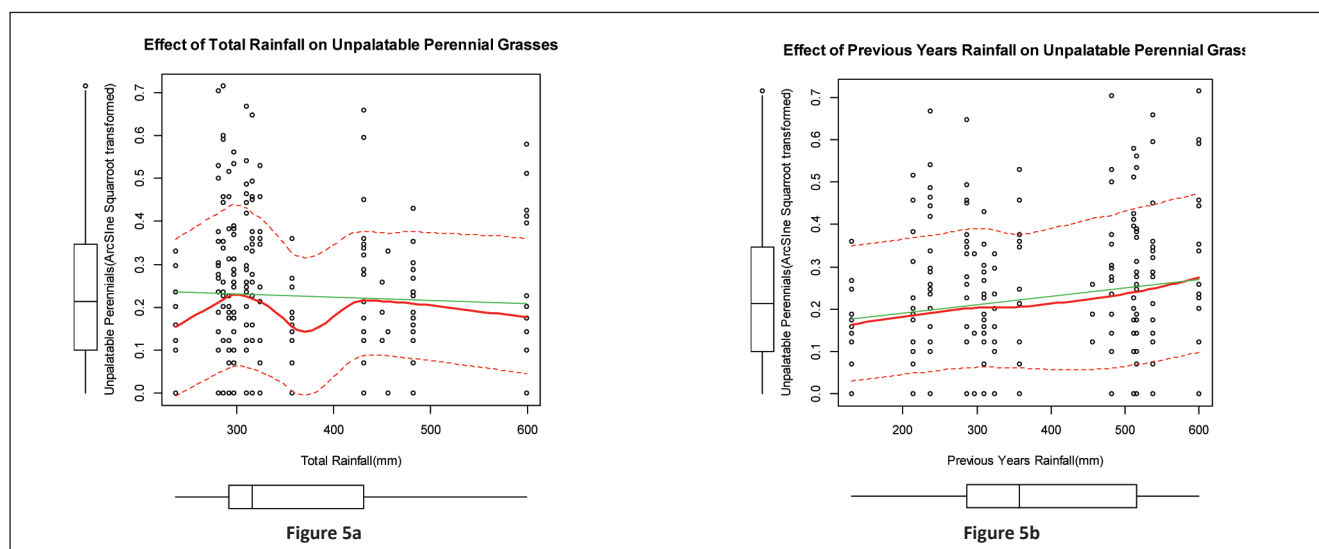


FIGURE 5: Unpalatable perennial grasses vs. (a) total rainfall (b) previous rainfall

The overall weak pattern of response of palatable perennial grasses is explained in part by the contrasting responses of dominant species. The most abundant palatable perennial grass, *Schmidtia pappophoroides*, strongly influenced the abundance of this group; this species decreased in response to increased rainfall of either seasonal component (Figure 6a, b) and rainfall of the previous year (Figure 6c), and to increasing soil depth (Figure 6d). However, an interesting possible trend with *Schmidtia pappophoroides* was detected. It seems that *Schmidtia pappophoroides* increases with a rainfall peak (more than 100 mm in one month) in one month during January–March rainfall season (Figure 7). By

contrast, *Themeda triandra* increased with increasing rainfall of the previous year (Figure 8a), and also increased over time (Figure 8b). Another conspicuous palatable perennial grass *Eragrostis lehmanniana* did not show a clear response to rainfall but increased in response to soil depth (Figure 9a), decreased in response to soil clay (Figure 9b), and was most abundant at intermediate levels of their interaction level. *Stipagrostis uniplumis* did not show a significant response to any factor. Starkly different responses of the four main palatable perennial grass species therefore preclude a uniform response of this functional group.

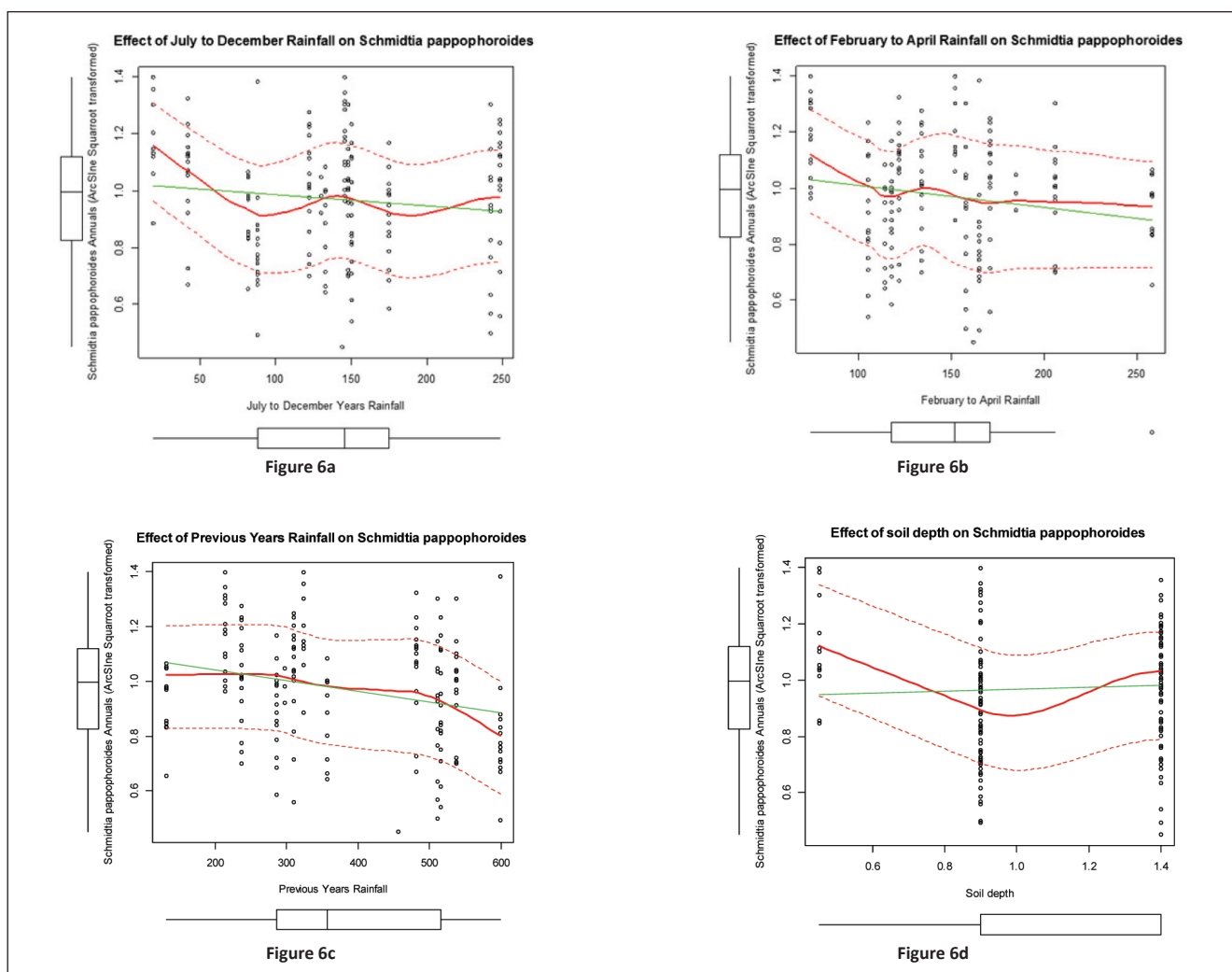


FIGURE 6: *Schmidtia pappophoroides* vs. (a) July to December rainfall (b) February to April rainfall (c) rainfall of the previous season (d) soil depth

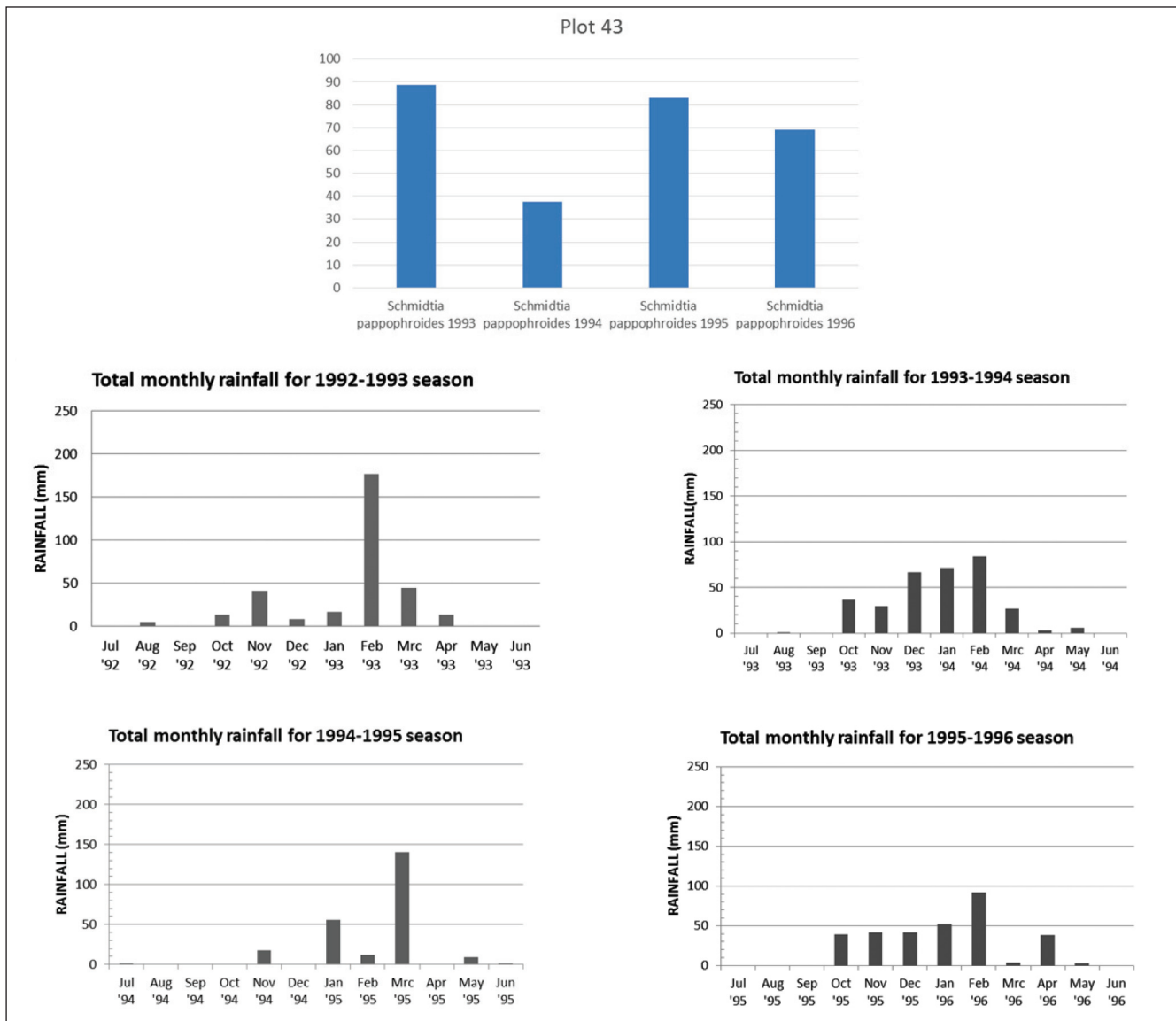


FIGURE 7: The increase trend of *Schmidtia pappophroides* closely associated with rainfall peak during four years (1993–1996) rainfall

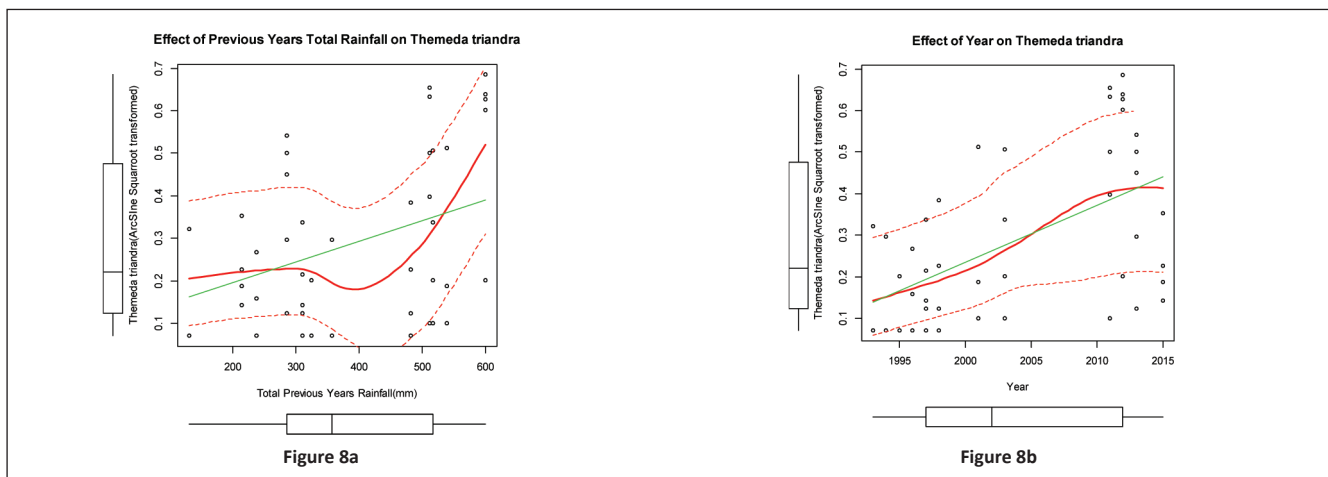


FIGURE 8: *Themeda triandra* vs. (a) rainfall of previous season (b) annual rainfall year

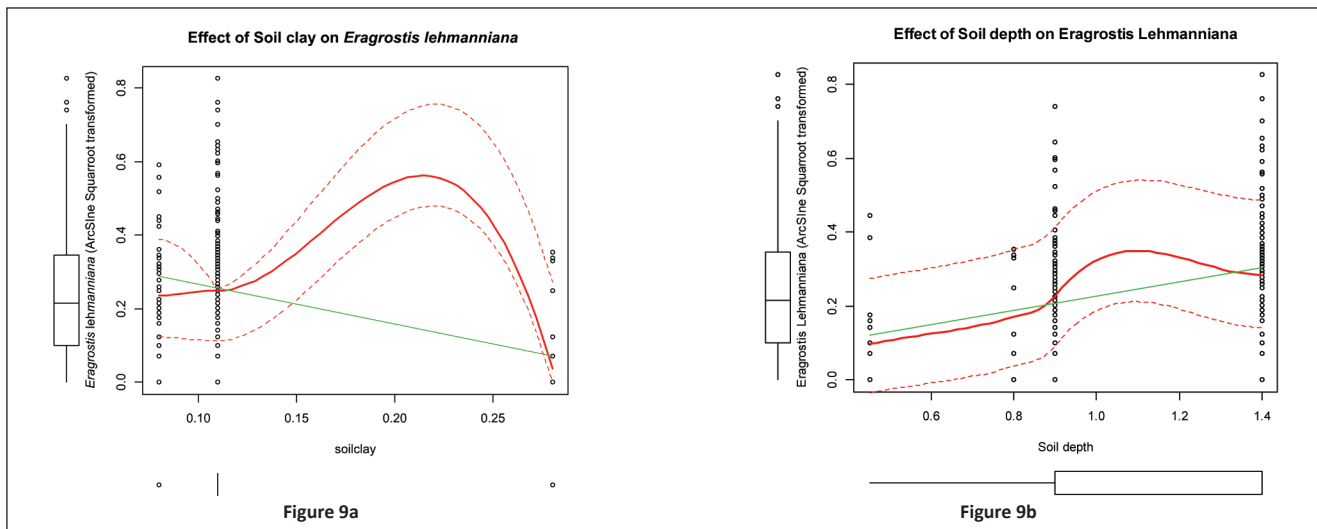


FIGURE 9: *Eragrostis lehmanniana* vs. (a) soil clay (b) soil depth

Palatable annual grasses did not respond in the same manner as unpalatable annual grasses. Unpalatable annual grasses increased in response to increased total rainfall (Figure 10a), specifically to increased February–April rainfall (Figure 10b), and increased slightly between 1993 and 2015 (Figure 10c). By contrast, palatable annual grasses

were considerably more abundant on clay-rich than sandy soils (Figure 11), becoming prolific on shallow but not deep soils during years of high rainfall (interaction term; Table 3). Neither dwarf shrubs nor perennial forbs showed any significant responses; annual forbs and geophytes could not be analysed owing to small sample sizes.

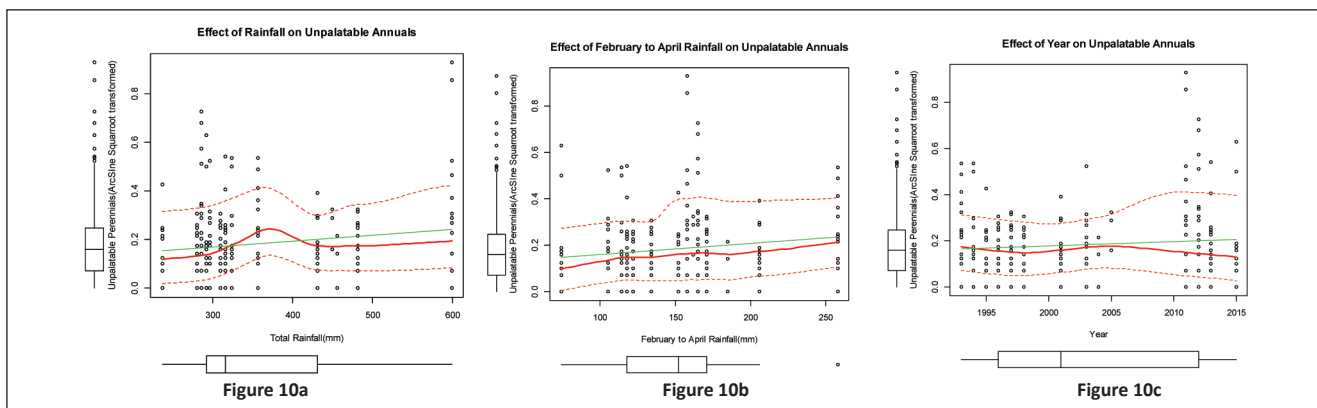


FIGURE 10: Unpalatable annual grasses vs. (a) total rainfall (b) rainfall of February to April (c) annual rainfall year

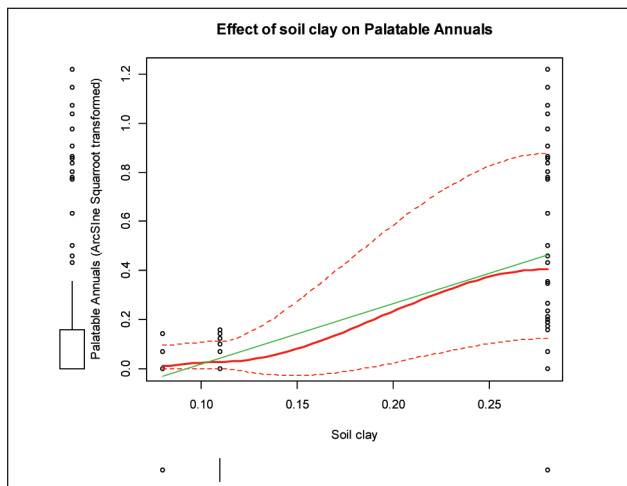


FIGURE 11: Palatable annual grass species vs. soil clay content

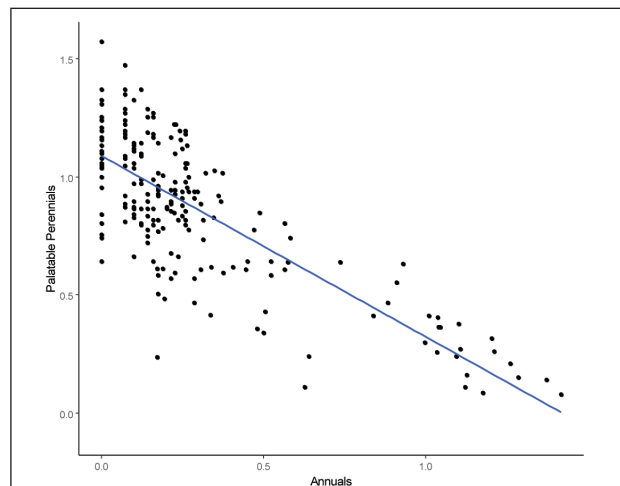


FIGURE 12: Negative relation between palatable perennial and annual grass species

The unexpected decline of palatable perennial grasses in response to increasing rainfall was influenced in part by use of relative rather than absolute abundance, as shown by a negative relation between palatable perennial and annual grasses (Figure 12). This indicates that in wet years annual

grasses proliferated between perennial grass tufts and were therefore measured as closest to point of sampling. This influence of annual grasses obscures whether perennial grasses changed in absolute terms.

TABLE 3: Summary of the general linear model results for the response of plant growth forms and individual dominant species to rainfall and soil variables. *Key to variables:* 'Rainfall', rainfall of the current season (July–April inclusive); 'Previous rainfall', rainfall of the previous season (July–June inclusive); 'July–December rainfall', current season's rainfall for these months (early season); 'February–April rainfall', current season's rainfall for these months (late season); 'Soil depth', depth of soil column; 'Soil clay', percentage clay content and a surrogate index of soil fertility; 'Depth-by-clay', surrogate index of potential amount of water in soil column or of soil fertility; 'Rainfall x depth-by-clay', surrogate index of the amount of water available to plants in that season; 'Year', reflects potential directional trend over time.

Vegetation variable	Environmental variable	Change in AIC	chi	df	P
Palatable perennial grasses	Rainfall	2.130	4.1395	1	0.0419
	Previous rainfall	4.98	6.9773	1	0.0083
Unpalatable perennial grasses	Rainfall	1.38	3.38	1	0.0659
	Previous rainfall	10.45	12.46	1	0.0004
	July–December rainfall	7.66	9.66	1	0.0019
	Rainfall x depth-by-clay	7.27	9.28	1	0.0023
<i>Eragrostis lehmanniana</i>	Soil clay	5.30	7.30	1	0.0069
	Soil depth	2.80	4.80	1	0.0285
	Depth-by-clay	3.01	7.00	2	0.0301
	Rainfall x depth-by-clay	1.52	5.52	2	0.0634
<i>Schmidtia pappophoroides</i>	Previous rainfall	12.25	14.25	1	0.0002
	July–December rainfall	13.98	15.98	1	6.40e-05
	February–April rainfall	24.19	26.19	1	3.09e-07
	Soil depth	0	0	0	< 2.2e-16
<i>Themeda triandra</i>	Previous rainfall	7.13	9.13	1	0.0025
	Year	32.859	3	1	3.55e-09
Unpalatable annuals	Rainfall	7.63	11.62	2	0.0030
	February–April rainfall	3.12	5.12	1	0.0236
	Year	4.76	6.75	1	0.0093
Palatable annuals	Soil clay	11.57	19.57	4	0.0006
	Rainfall x depth-by-clay	1.11	1.10	0	2.2e-16

Discussion

Inter-annual rainfall variation

Study of the influence of inter-annual rainfall variation on the dynamics of herbaceous vegetation usually has to rely on long-term monitoring data sets because manipulation of rainfall is impracticable. When using monitoring data, relating vegetation changes to rainfall variation requires that the effect of other potential agents of vegetation change can be discounted. In this study of Vaalbos, grazing pressure was usually within recommended norms, fire was infrequent and did not affect many transects, and there was no evidence of increasing woody cover over the 22-year monitoring period (Table 2). The data are therefore considered to highlight the influence of rainfall variation.

Inter-annual rainfall variability is a primary driver of compositional variation in savanna grassland (O'Connor 1985; Veenendaal *et al.* 1996a, b). Expectation that rainfall variation would influence variation of at least some plant functional groups and their constituent species was met for perennial grasses, some of their dominant species and palatable annual grasses but there were stark differences in response to total or seasonal (early versus late) rainfall,

rainfall of the previous season, soil water storage capacity, and soil fertility that appear influenced by growth form and life history strategy.

Rainfall is an indirect surrogate of plant available water (*sensu* Austin & Smith 1989) because the availability of rainfall to plants is mediated by the effect of soil depth and texture on soil water storage (Ritchie 1981; Foth 1990). The amount of water stored, but also the amount of water held back from plants per unit volume of soil, increases with increasing clay content resulting in deep, sandy soils offering less in absolute terms but the most stable amount, and clay soils offering potentially the largest but also the most variable amount of soil water over time. As a consequence for southern African savannas, botanical composition of sandveld is more stable than that of high clay-content textured soils in response to inter-annual rainfall variability (Dye & Spear 1982; O'Connor 1985). The soil texture and soil depth of a soil plays an important role in storing water, with the sandy soil being deeper than that of the higher clay-content soil. Therefore the sandy soils will have more water available and longer available in time, than that of the more clayey content soil (Hillel 1971) of Vaalbos. To our knowledge, an effect of soil water

storage on temporal variation in the abundance of plant species or groups has not previously been shown. In this study, a significant positive interaction between rainfall and a product of depth and soil texture was evidence for an effect of soil water storage on the abundance of unpalatable perennial grasses, the most abundant species of this group *Pogonarthria squarrosa*, and the most abundant palatable perennial grass species *Schmidtia pappophoroides* (Table 3).

An effect of rainfall of the preceding season for both palatable and unpalatable perennial grasses, as well as for two individual palatable species (Table 3), indicates a 'carry-over' effect from one season to the next (O'Connor *et al.* 2001). Whether carry-over occurs as a result of soil water storage or through an enhanced physiological condition of the plants is not known. Three other perennial grasses *Eragrostis lehmanniana*, *Stipagrostis uniplumis*, and *Pogonarthria squarrosa*, dwarf shrubs and perennial forbs did not show a carry-over effect. These contrasting responses preclude a conclusion as to whether a carry-over effect is most likely to occur with certain functional groups or on only some soil types.

Plant available nutrients and water are the two primary determinants of the structure and organisation of African savannas (Frost *et al.* 1986) whose separate effects on plants are difficult to identify owing to both being determined by soil texture (Foth 1990). However, use of an interaction term which represented the effect of soil water storage in our models meant that an effect of soil texture without any effect of the soil water storage term was evidence of an effect of nutrient availability. This was observed for the perennial grass *Themeda triandra*, whose distribution in semi-arid savannas is related to heavy textured soils (Mucina & Rutherford 2006). For example on catenas in granite landscapes in southern African savanna, this species is absent from their sandy crests but conspicuous on the heavy-textured bottomlands (Bredenkamp *et al.* 1983).

Effect of early versus late season rainfall

Semi-arid savanna in southern Africa is dominated by perennial grasses except when degraded, with annual grasses usually a minor component in mesic regions (Mucina & Rutherford 2006). Expectation that their appearance and, when present, their abundance, would depend on rainfall during the first half of the season in order to ensure their life cycle could be completed, was met for palatable annual grasses. In contradiction of expectation, abundance of unpalatable annual grasses was related to the amount of rainfall for the late season (Figure 10). A possible explanation is that the group of unpalatable annual grasses was dominated by *Aristida congesta* subsp. *congesta* which is not a true annual but behaves as a short-lived perennial when conditions allow (Van Oudtshoorn 1999). Unfortunately there were insufficient data by which to examine the response of annual forbs.

Although annual grasses are expected to respond to early versus late season rainfall, we know of no evidence for a

similar response by perennial grasses in semi-arid savannas in southern Africa. No perennial groups responded to early season rainfall as annuals did, but two species of palatable grass, *Schmidtia pappophoroides* and *Themeda triandra*, both responded, but in an opposite manner. Abundance of *Schmidtia pappophoroides* increased whereas that of *Themeda triandra* declined if February–April rainfall was high (Figure 6b). The observed pattern was counter-intuitive because *Schmidtia pappophoroides* is a common dominant in the western regions (Mucina & Rutherford 2006) where the summer rainfall peak occurs late in summer (February–April) (Tyson & Preston-Whyte 2000). By contrast, *Themeda triandra*, which responded most to late season rainfall, is a dominant of many eastern savannas (Mucina & Rutherford 2006) where rainfall peaks in mid-summer (November–February). Long-term shifts in the seasonal distribution of rainfall, such as recorded in the Nama-Karoo (Du Toit & O'Connor 2014), should result in conspicuous reorganisation of plant community composition.

Coexistence of different growth forms

Savannas are defined as a mixture of trees and grasses whose functioning is determined primarily by plant-available moisture and available nutrients, and secondarily by fire and herbivory (Frost *et al.* 1986). Explanation of the coexistence of these two growth forms has been a central pursuit of savanna ecologists for over a half century (Sankaran *et al.* 2004; O'Connor *et al.* 2014). Forbs (herbaceous dicotyledons and non-graminoid monocotyledons) tend to be overlooked – although they usually contribute a small amount to total savanna biomass they constitute a disproportionate amount of total species richness (Zietsman & Bezuidenhout 1999). Explanation of the coexistence of growth forms in savannas should therefore be expanded to include forbs. Patterns of soil water use was conspicuously different between trees, grasses, and forbs in a semi-arid southern African savanna in Zimbabwe (Clegg & O'Connor 2017). Each group required different volumes of soil water to produce green material, and woody plants and forbs responded to long-term changes in soil moisture whereas grasses responded to short-term moisture pulses. This study provides further evidence of the importance of plant-available water on the coexistence of different plant functional groups but more detailed monitoring methods than the wheel-point method that was used are needed. So far in South Africa, the wheel-point method is being successfully used for agricultural pastures with homogenous veld, but this will need some major adjustments of the method for heterogeneous veld, as was pointed out by this study.

Implications for management

A key challenge facing management of grazed semi-arid savanna has been to increase palatable perennial grasses, for which rainfall variation may provide windows of opportunity and discrete threats (Westoby *et al.* 1989). For a Zimbabwean semi-arid savanna, a model of species' growth indicated that these grasses were best maintained

over the long term in the face of inter-annual rainfall variation using a conservative stocking strategy (Dye 1983). Field measurement revealed that differences in the timing of rainfall within a season benefitted different perennial grass species (Dye & Walker 1987), on which basis it was suggested that management could schedule grazing according to rainfall and phenological considerations in order to direct changes in species composition and increases in yield (Walker *et al.* 1986). This suggestion applies to this study – rainfall of the current or preceding season, amount of early or late season rainfall, and soil water storage capacity can potentially be taken into consideration for directing change in most growth forms or individual perennial species. Specifically, palatable perennial grasses responded to rainfall of both the current and preceding season, as well as to soil (Figures 4a and 4b).

Bush densification (La Grange 2010) is undesirable for semi-arid savanna because of its effect on grass production (O'Connor & Stevens 2017), but no densification of the indigenous woody plant species did occur nor did any new woody species enter over 22 years (Figure 3; Table 2) despite considerable variation in rainfall. Rainfall variability may promote bush densification through its effect on grazing pressure and fire frequency (O'Connor *et al.* 2014), and densification can be expected on Kalahari sands under sustained grazing (Wiegand *et al.* 1998), but this did not occur on the study area (Figure 3). Instead, the response resembled the relatively constant abundance of woody plants recorded on Kalahari sands in the Kalahari Gemsbok National Park over years (Van Rooyen *et al.* 1984).

Conclusion

Botanical composition is routinely used in southern Africa for assessing rangeland condition because composition indicates potential forage value (Tainton 1999). Inter-annual rainfall variability has long been recognised as a primary influence on herbaceous vegetation dynamics in semi-arid regions (O'Connor 1985) that may portend opportunities or threats regarding vegetation change by management (Westoby *et al.* 1989). Although variable rainfall was found to have an expected, conspicuous effect on composition, key functional groups or species showed differences in response that depended for some on previous year's rainfall, soil water storage, or within-season rainfall distribution. Management could utilise predicted spatial and temporal differences for anticipating forage availability through the season or for alleviating herbivore impact on certain components. Insights derived from this study support the maintenance of similar monitoring efforts for managing other rangelands, a number of which have apparently been abandoned in recent time. For such monitoring to be successful, vegetation-environment relations need to have been described and climate needs to be monitored. The possible trend that was observed with *Schmidtia pappophoroides* needs to be investigated but the method should be adapted and lessons from this long-term study should be implemented.

The greatest challenge facing conservation-relevant monitoring is balancing the development of appropriate strategies with personnel, time and budget constraints (Buckley *et al.* 2008; Walker 2009). In fact, the monitoring that is carried out in protected areas has been shown to be more strongly correlated with resource availability than any other factor (Bruner *et al.* 2001; WWF 2004). Lack of human capacity, time and budget constraints are probably the main reasons for the lack of publication of ecological monitoring data in conservation areas.

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APPENDIX 1: Species sampled within each functional group

Functional group	Species
Palatable perennial grasses	<i>Antheophora pubescens</i> , <i>Brachiaria serrata</i> , <i>Cynodon dactylon</i> , <i>Enneapogon desvauxii</i> , <i>Eragrostis bicolor</i> , <i>Eragrostis echinochloidea</i> , <i>Eragrostis lehmanniana</i> , <i>Eragrostis obtusa</i> , <i>Eragrostis rotifer</i> , <i>Eragrostis x pseud-obtusa</i> , <i>Heteropogon contortus</i> , <i>Panicum coloratum</i> , <i>Schmidtia pappophoroides</i> , <i>Sporobolus ioclados</i> , <i>Stipagrostis ciliata</i> , <i>Stipagrostis uniplumis</i> , <i>Themeda triandra</i> , <i>Tragus koelerioides</i> , <i>Tricholaena monachne</i> , <i>Urochloa mosambicensis</i>
Unpalatable perennial grasses	<i>Aristida meridionalis</i> , <i>Aristida stipitata</i> , <i>Eragrostis pallens</i> , <i>Eragrostis trichophora</i> , <i>Pogonarthria squarrosa</i>
Palatable annual grasses	<i>Chloris virgata</i> , <i>Cyperus species</i> , <i>Melinis repens</i> , <i>Setaria verticillata</i> , <i>Sporobolus coromandelianus</i> , <i>Tragus berteronianus</i> , <i>Tragus racemosa</i> , <i>Urochloa panicoides</i>
Unpalatable annual grasses	<i>Aristida adscensionis</i> , <i>Aristida congesta</i> subsp. <i>barbicollis</i> , <i>Aristida congesta</i> subsp. <i>congesta</i> , <i>Aristida diffusa</i> , <i>Bulbostylis humilis</i> , <i>Eragrostis porosa</i>
Dwarf shrubs	<i>Chrysocoma ciliata</i> , <i>Elephantorrhiza elephantina</i> , <i>Felicia fascicularis</i> , <i>Felicia muricata</i> , <i>Gnidia polycephala</i> , <i>Helichrysum lucilioides</i> , <i>Hermannia tomentosa</i> , <i>Lycium cinereum</i> , <i>Pentzia incana</i> , <i>Plinthus sericeus</i> , <i>Pollichia campestris</i> , <i>Rosenia humilis</i> , <i>Salsola calluna</i> , <i>Salsola rabieana</i> , <i>Selago densiflora</i> , <i>Solanum tomentosum</i>
Perennial forbs	<i>Aptosimum albomarginatum</i> , <i>Aptosimum lineare</i> , <i>Barleria bechuanensis</i> , <i>Commelina africana</i> , <i>Convolvulus multifidus</i> , <i>Corchorus asplenifolius</i> , <i>Cullen tomentosum</i> , <i>Dicoma schinzii</i> , <i>Gazania linearis</i> , <i>Heliotropium lineare</i> , <i>Heliotropium steudneri</i> , <i>Indigofera daliooides</i> , <i>Indigofera vicioides</i> , <i>Kohautia cynachica</i> , <i>Lotononis platycarpa</i> , <i>Nolletia ciliaris</i> , <i>Rhynchosia venulosa</i> , <i>Ruellioopsis setosa</i> , <i>Talinum caffrum</i> , <i>Vahlia capensis</i>
Annual forbs	<i>Amaranthus praetermissus</i> , <i>Cleome rubella</i> , <i>Gesekia pharnaceoides</i> , <i>Limeum fenestraum</i> , <i>Nidorella resedifolia</i> , <i>Tephrosia burchellii</i>
Geophytes	<i>Oxalis depressa</i>