Woody vegetation change over more than 30 years in the interior duneveld of the Kalahari Gemsbok National Park

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Background and objectives: Long-term studies of woody plants in South Africa are scarce. This study, initiated in the late 1970s, therefore aids understanding of vegetation dynamics in the southern Kalahari by investigating woody vegetation change at and away from a watering point.

Methods: At three sites, all woody individuals were counted by species in plots 0.5 or 1 ha in size. Seedlings were noted separately from the >0.2 m group of individuals.

Results: *Vachellia erioloba* and shrub density decreased over time whereas dwarf shrub species' numbers fluctuated markedly. Additionally, no increase in density of known bush encroaching species (e.g. *Grewia flava*, *Rhigozum trichotomum* and *Senegalia mellifera*) was found in this large conservation area.

Discussion and conclusion: The changes in density of the woody species seem to point to the importance of particular rainfall patterns or sequences of events over different years that are responsible for these changes in the southern Kalahari, and the evident lack of bush encroachment in this conservation area supports the notion that bush encroachment in arid savannas is driven primarily by land-use practices and not by elevated carbon dioxide levels that are sometimes provided as cause for encroachment.

Key words: bush encroachment, conservation area, Kgalagadi Transfrontier Park, southern Kalahari, *Vachellia erioloba*, vegetation dynamics, watering point.

Introduction

Detecting environmental change at multiple spatial and temporal scales through biotic and abiotic research is of crucial importance not only to policymakers and scientists, but also to natural resource managers (Haase et al. 2018; Parr et al. 2002; Peters et al. 2014). Long-term monitoring can be used as a tool to assess the past management of natural resources, but also provides an understanding of ecological patterns and processes, which can improve decisions on the management of ecosystem assets (Lindenmayer & Likens 2009).

Lindenmayer and Likens (2010) identified three broad, long-term monitoring approaches, these are: (i) curiosity-driven or passive monitoring; (ii) mandated monitoring; and (iii) question-driven monitoring. The first type, passive monitoring, usually has no specific questions or underlying study design and has limited rationale other than curiosity, while the second type, mandated monitoring, is a requirement of government legislation or a political directive. Question-driven monitoring, the third type, generally tests predictions that are guided by a conceptual model and rigorous design. The categories are, however, not mutually exclusive.

There are still relatively few biodiversity time-series that span decades (Magurran et al. 2010) and this is particularly true for woody species (Moustakas et al. 2008). In the southern hemisphere, observational networks and research investment are largely lacking, and therefore even relatively short-term current and archived historical data sets can provide baselines for investigating change (Chambers et al. 2016).

Numerous surveys were initiated in the Kalahari Gemsbok National Park (KGNP) [now part of the Kgalakgadi Transfrontier Park (KTP)] to document vegetation change from 1978 onwards. The aim of this paper is to report on the monitoring that was initiated at three sites after a number of years with above-average rainfall, and follows a passive monitoring approach. The principal questions asked at the time were: how does the woody vegetation change at and away from a watering point, and what is the rate of survival at each of the sites? Although the research was not hypothesis driven (Lindenmayer & Likens 2010), monitoring was conducted over nearly four decades and therefore the data warrant exploration and reporting.

Study area

The study was conducted in the KGNP in South Africa. The KGNP covers about 9 600 km² and is situated between 24°15′ S and 26°30′ S and 20°00′ E, and 20°45′ E in the southwestern corner of the Kalahari region (Van Rooyen et al. 2008). Monitoring was conducted at three sites in the vicinity of the Dankbaar watering point, which was opened in 1959 (Figure S1). The study sites were situated within the *Acacia* (*Vachellia*) *erioloba*–*Schmidtia kalahariensis* Low Duneveld (Van Rooyen et al. 2008). This open tree savanna occurs in the interior duneveld in the northern part of the park. The vegetation is dominated by *V. erioloba* and *S. kalahariensis* (grass), with other prominent woody species being *Boscia albitrunca*, *Rhigozum trichotomum* and *Senegalia mellifera*.

Rainfall is received mainly in late summer with a mean of 194 mm/yr recorded from 1976 to 2015 at Nossob Rest Camp (Figure S2). The rainfall is highly erratic (standard deviation ± 88.8 mm) and occurs primarily from January to April, with a peak in March. Temperatures show a large amplitude with winter lows reaching -10.3°C and summer highs reaching 45.4°C (Van Rooyen & Van Rooyen 1998).

Methods

Study sites

Three study sites were established in the interior duneveld between 1978 and 1982. The first site was 5 km

to the east of the watering point (25°03′39.13″ S and 20°07′17.37″ E) (hereafter referred to as EoWP) and monitoring commenced in 1978. The second site, at the Dankbaar watering point, (25°04′10.90″ S and 20°05′47.50″ E) (hereafter referred to as WP), was monitored for the first time in 1980. At the third site, 5 km to the north of the watering point, (25°01′39.45″ S and 20°05′0.30″ E) (hereafter referred to as NoWP), monitoring started in 1982. At the time when monitoring commenced, WP was dominated by a dense stand of *V. erioloba* saplings; NoWP had an intermediate density of relatively young *V. erioloba* individuals; whereas EoWP was a mixed stand of mature *V. erioloba* and *Vachellia luederitizii* individuals at a low density. The plots at WP and NoWP were 0.5 ha in size, while the plot EoWP was 1 ha in size. In each plot, all woody individuals were counted by species. Additionally, seedlings (individuals <0.2 m tall) were noted separately from the sapling and mature group of individuals (>0.2 m individuals). All three plots were monitored intermittently, i.e. WP sampled 16 times, NoWP 14 times and EoWP 9 times, including the initial and 2016 surveys.

Statistical analysis

To visualise change in density over time at the different sites, we used linear regressions with the natural log (=ln) density (number of individuals/ha) per species over time (survey years), in the package Graphpad Prism (version 5, graphpad.com). Data for each site were analysed separately. Only species that occurred in the plots on four or more occasions were included in the analyses i.e. a minimum of four data points.

A linear regression of (a) seasonal; (b) annual; or (c) the cumulative annual rainfall of the previous three years against the annual change in tree density between two survey years was investigated.

Results

Generally, the density of tree species declined over the monitored period (Table 1). Furthermore, this decline was significant for *Vachellia erioloba* individuals (>0.2 m) at WP and NoWP (Figure 1a). Additionally, the seedlings (< 0.2 m) of *V. erioloba* decreased significantly at WP (Figure 1b).

For the numerous shrub species counted in the plots during the monitoring period (Table 1), shrub density declined significantly for only three shrub species i.e. *Ehretia alba*, *Lycium bosciifolium* and *Rhigozum trichotomum*. Densities of *E. alba* showed a significant decrease at WP and EoWP (Figure 2a). *Lycium bosciifolium* density decreased significantly at WP (Figure 2b). *Rhigozum trichotomum* density also declined significantly NoWP (Figure 2c).

Table 1: Equations, r²- and p-values of the polynomial regressions fitted to the density data at three sites (watering point, north of watering point and east of watering point) illustrated in figures 1, 2 and 3. Only species with a minimum of four data points were used in the analyses.

| Species	Watering point (WP)	5 km north of watering point (NoWP)	5 km east of watering point (EoWP)
Trees			
Boscia albitrunca	$y = 0.0069x + 17.323$, $r^2 = 0.015$, $p = 0.650$	$y = 0.002x - 3.684$, $r^2 = 0.011$, $p = 0.730$	$y = -1.4E^{-05}x + 3.301$, $r^2 = 1.11E^{-07}$, $p = 0.999$
Vachellia erioloba (sapling/mature)	$y = -0.040x + 84.232$, $r^2 = 0.383$. $p = 0.011$*	$y = -0.040x + 84.711$, $r^2 = 0.0907$, $p = 1.52E^{-07}$***	$y = -0.033x + 68.864$, $r^2 = 0.272$, $p = 0.1499$
Vachellia erioloba (seedlings)	$y = -0.377x + 752.291$, $r^2 = 0.617$, $p = 0.021$*	$y = 0.022x - 42.021$, $r^2 = 0.025$, $p = 0.801$	$y = -0.002x + 5.338$, $r^2 = 0.005$, $p = 0.972$
Vachellia haematoxylon	$y = 0x + 0.693$, $r^2 = 1$	$y = 0.017x - 32.452$, $r^2 = 0.137$, $p = 0.293$	-
Vachellia luederitzii (sapling/mature)	$y = -0.065x + 122.126$, $r^2 = 0.439$, $p = 0.007$	-	$y = -0.020x + 43.232$, $r^2 = 0.679$, $p = 0.006$**
Vachellia luederitzii (seedlings)	-	-	$y = -0.503x + 1000.157$, $r^2 = 0.600$, $p = 0.124$
Shrubs			
Ehretia alba	$y = -0.079x + 159.184$, $r^2 = 0.697$, $p = 0.0001$***	-	$y = -0.030x + 62.889$, $r^2 = 0.0527$, $p = 0.027$*
Grewia flava	$y = -0.012x + 25.484$, $r^2 = 0.0018$, $p = 0.633$	-	$y = 0.0167x - 30.388$, $r^2 = 0.118$, $p = 0.406$
Grewia retinervis	$y = 0.065x - 127.501$, $r^2 = 0.206$, $p = 0.365$	-	$y = -0.008x + 18.888$, $r^2 = 0.002$, $p = 0.916$
Lycium bosciifolium	$y = -0.067x + 136.606$, $r^2 = 0.390$, $p = 0.013$*	-	$y = -0.038x + 79.961$, $r^2 = 0.331$, $p = 0.233$
Rhigozum trichotomum	$y = -0.0258x + 55.088$, $r^2 = 0.189$, $p = 0.093$	$y = -0.051x + 104.018$, $r^2 = 0.534$, $p = 0.001$**	$y = -0.019x + 44.091$, $r^2 = 0..398$, $p = 0.093$
Searsia tenuinervis	-	-	$y = 0.028x - 55.349$, $r^2 = 0.397$, $p = 0.130$
Senegalia mellifera (mature)	-	-	$y = -0.010x + 19.963$, $r^2 = 0.091$, $p = 0.429$
Senegalia mellifera (seedlings)	-	-	-
Dwarf shrubs			
Aptosimum albomarginatum	-	-	$y = -0.114x + 232.37$, $r^2 = 0.978$, $p = 0.011$*
Asparagus nelsii	-	$y = -0.028x + 59.187$, $r^2 = 0.378$, $p = 0.019$*	-
Chrysocoma obtusata	$y = 0.091x - 178.253$, $r^2 = 0.376$, $p = 0.059$	-	-
Hermannia burchelli	-	-	-
Hermannia tomentosa	-	-	-
Justicia incana	$y = -0.095x + 193.492$, $r^2 = 0.474$, $p = 0.013$*	-	$y = -0.111x + 227.312$, $r^2 = 0.754$, $p = 0.005$**
Plinthus sericeus	$y = 0.038x + 73.733$, $r^2 = 0.217$, $p = 0.293$	$y = 0.069x - 135.134$, $r^2 = 0.247$, $p = 0.100$	-
Pollichia campestris	$y = -0.034x + 71.169$, $r^2 = 0.190$, $p = 0.119$	$y = -0.038x + 79.328$, $r^2 = 0.395$, $p = 0.016$	-
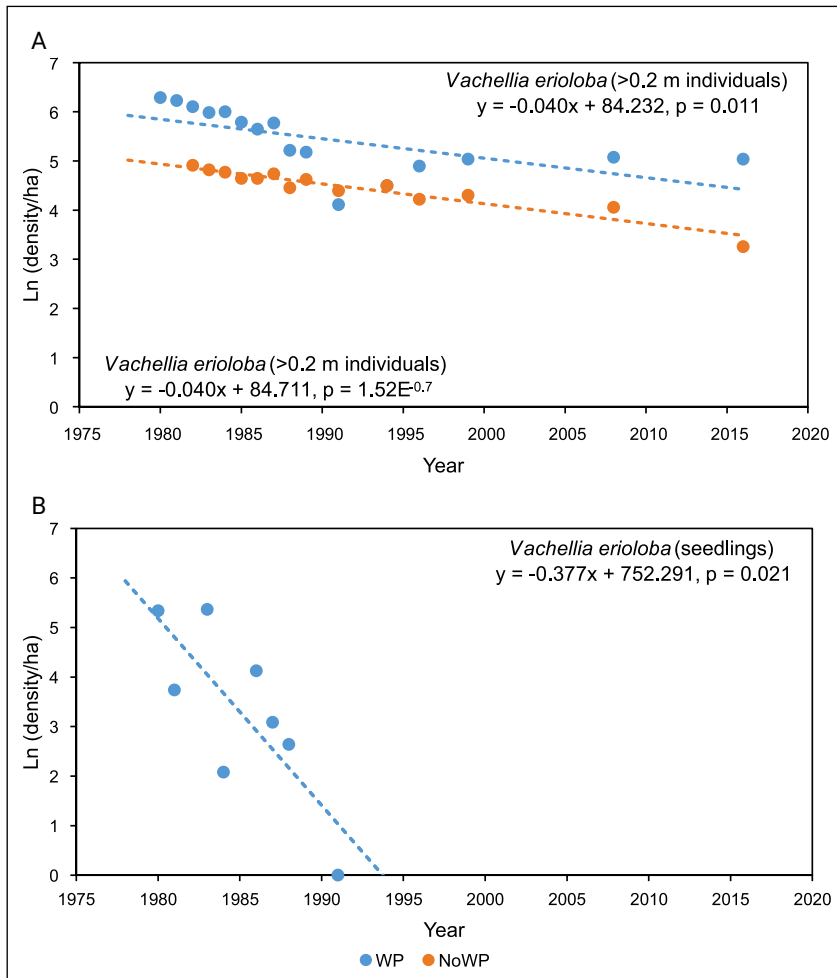
Figure 1. Linear regressions of the natural logarithm of the number of individuals per hectare, indicating significant trends in density of *Vachellia erioloba* over time. (a) >0.2 m individuals, and (b) seedlings. WP = Watering point, NoWP = North of watering point.

Overall, the dwarf shrub species showed large fluctuations in density over the monitored period, with no clear trends evident (Table 1). The density of *Asparagus nelsii* (EoWP), *Aptosimum albomarginatum* (NoWP), *Justicia incana* (WP, EoWP) and *Pollichia campestris* (NoWP) decreased significantly over the monitoring period (Figure 3).

No relationship between tree density and seasonal or annual rainfall or the cumulative annual rainfall of the previous three years was found. This does not exclude rainfall as driving factor, but seems to point towards the effect of a particular rainfall pattern or sequence of events over different years that is responsible for changes in tree densities.

Discussion

The authors acknowledge that this study was limited by the number of sites lacking replication and the possibility that individuals were missed during the field surveys, however the length of the study warrants exploration of the data set.

The most outstanding feature of this long-term data set is the significant decrease in density of *V. erioloba*

(>0.2m) individuals at two sites (WP, NoWP) (Figure 1). The most prominent decline was for *V. erioloba* at WP from the early 1980s until the mid-1990s, a period when the mean annual rainfall was below average for most years (Figure S2). This dry period followed on a wet cycle in the late 1970s that preceded the surveys. The large numbers of seedlings could have been the aftermath of the wet cycle and their demise as a result of the following dry cycle in the 1980s. Numerous authors have reported large numbers of *V. erioloba* seedlings following above average rainfall periods (Barnes 2001a, Moustakas et al. 2008, Seymour 2008), however, survival of *V. erioloba* seedlings is very low (Barnes 2001b, Seymour & Milton 2003, Steenkamp et al. 2008, Van der Merwe et al. 2019) due to either drought, frost, herbivory or fire. The low survival of seedlings was supported by the results of this study.

When monitoring commenced, the density of the *V. erioloba* >0.2 m individuals was approximately five-fold higher at WP than to the north thereof and 36-fold higher than at EoWP. Such high densities of saplings are quite uncommon in the interior duneveld (*pers. obs.* N.v.R) and this raises the question as to whether the high densities are in some way associated with the watering point opened in 1959, 21 years prior to the commencement of vegetation monitoring. *Vachellia erioloba*
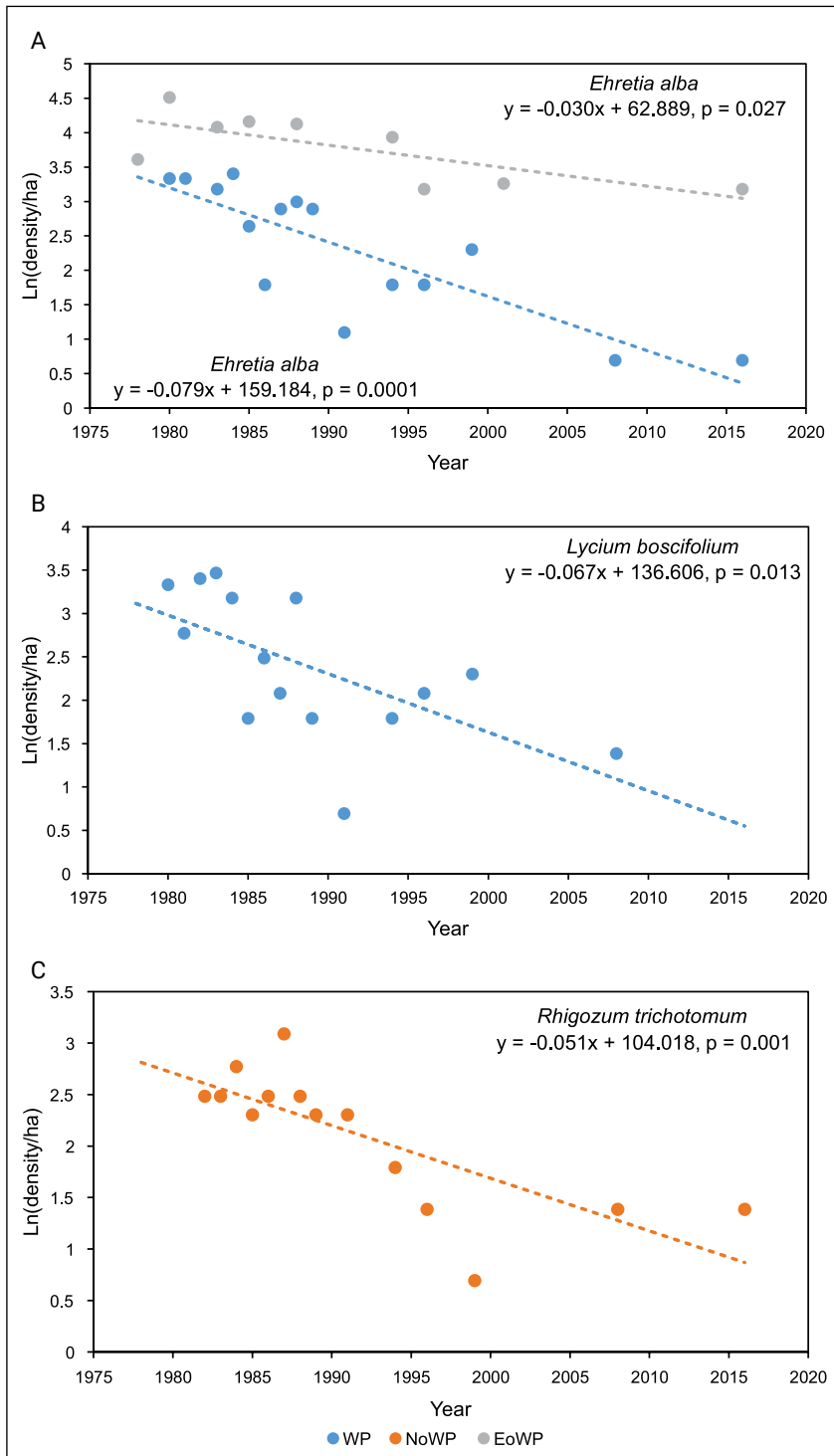
Figure 2. Linear regressions of the natural logarithm of the number of individuals per hectare indicating significant trends in density of shrub species over time. (a) *Ehretia alba*; (b) *Lycium bosciifolium*; and (c) *Rhigozum trichotomum*. WP = Watering point, NoWP = North of watering point, EoWP = East of watering point.

is often perceived by landowners as an encroaching species in the Kalahari (Seymour & Milton 2003) and it could be speculated that this species encroached at the watering point after it was opened and before monitoring started. However, the speculated encroachment did not continue during the monitoring period.

In 2016, the density of *V. erioloba* at WP was 29% and NoWP 19% of the initial density. It is therefore unlikely that borehole drawdown (Shadwell & February 2017) led to the dieback of trees at WP, since a similar

decrease also occurred away from the watering point. The large decrease in density in young individuals at WP and NoWP could largely be ascribed to density-dependent self-thinning, whereby density decreases with a concomitant increase in biomass of the remaining individuals (Silvertown & Charlesworth 2001).

At the three sites shrub densities generally decreased significantly or remained relatively constant. Three of these tall shrubby species are often associated with bush encroachment on heavily utilised farmland in the
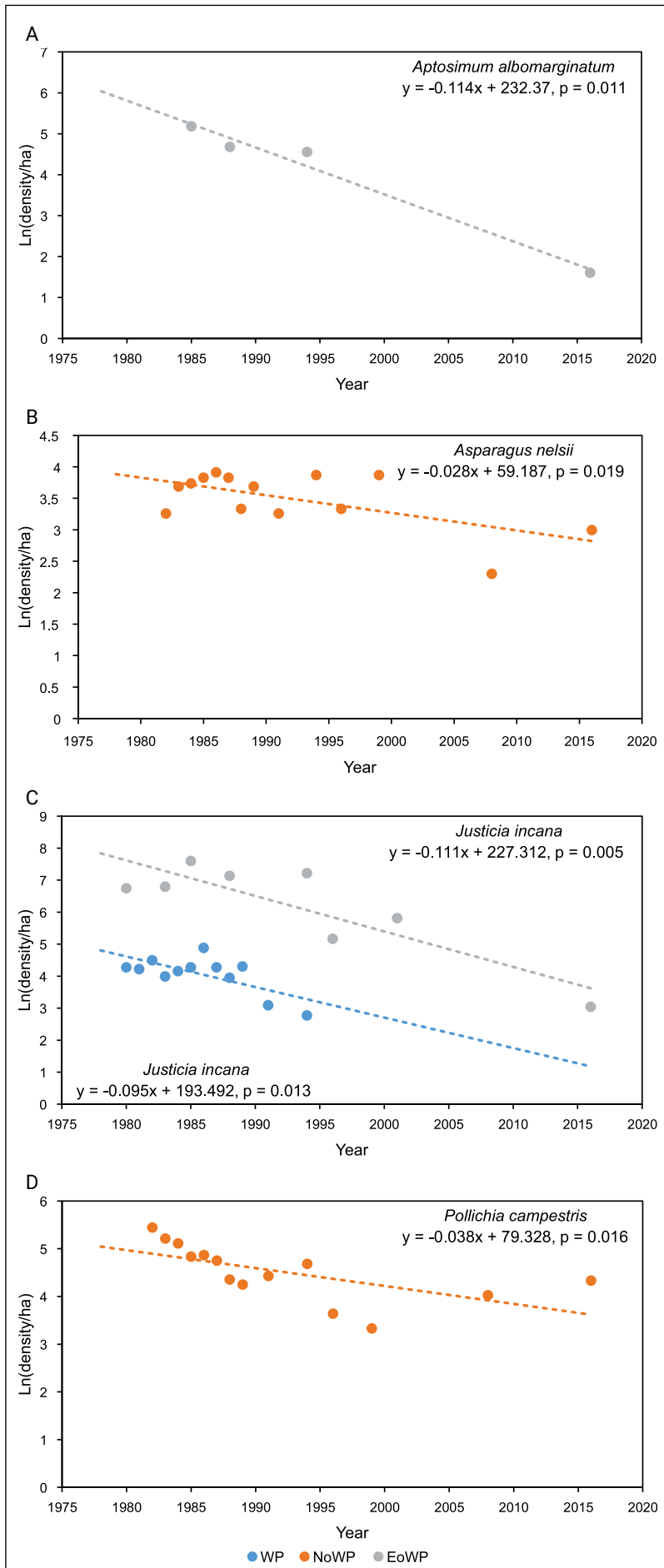
Figure 3. Linear regressions of the natural logarithm of the number of individuals per hectare indicating significant trends in density of dwarf shrub species over time. WP = Watering point, NoWP = North of watering point, EoWP = East of watering point. (a) *Aptosimum albomarginatum;* (b) *Asparagus nelsii*; (c) *Justicia incana*; and (d) *Pollichia campestris*.

Kalahari i.e. *Grewia flava*, *Rhigozum trichotomum* and *Senegalia mellifera* (Joubert et al. 2013, Moleele et al. 2002, Moore et al. 1988, Tews et al. 2004, Van Rooyen et al. 1994). However, densities of these known encroachers remained relatively constant (*G. flava* at WP and EoWP, *S. mellifera* at EoWP) or decreased significantly for *R. trichotomum* (NoWP) over the monitoring period at all sites.

The dwarf shrub densities showed large variability, as large as ten-fold, across the survey period. These fluctuations between high and low densities occurred at shorter time intervals than for the tree species.

Overall, the changes in density of the woody species seem to point to the importance of particular rainfall patterns or sequences of events over different years that are responsible for these changes in the southern Kalahari (Van Rooyen et al. 1990, 1994). Furthermore, the lack of evidence of bush encroachment in this conservation area at the three sites, one of which

is situated at a watering point, supports the notion that bush encroachment in arid savannas is driven primarily by land-use practices and not by elevated carbon dioxide levels that are sometimes provided as cause for encroachment (Nackley et al. 2018).

Conclusions

Monitoring was initiated based on a simple passive monitoring question of 'How does vegetation change over time?' The authors acknowledge that such research may be limited in usefulness as cautioned by Lindenmayer and Likens (2010), however, due to the length of the data set, investigation was justified. A similar decline in density of *V. erioloba* tree seedlings and >0.2 m individuals was found at and away from the watering point. Furthermore, the density of known bush encroaching species at the watering point did not increase over the monitored period.

References

Barnes, M.E., 2001a, 'Seed predation, germination and seedling establishment of *Acacia erioloba* in Northern Botswana', *Journal of Arid Environments* 49, 541–554, DOI: 10.1006/jare.2001.0805.

Barnes, M.E., 2001b, 'Effects of large herbivores and fire on the regeneration of *Acacia erioloba* in Chobe National Park, Botswana', *African Journal of Ecology* 39, 340–350, DOI: 10.1046/j.1365-2028.2001.00325.x.

Chambers, L.E., Barnard, P., Poloczanska, E.S., Hobday, A.J., Keatley, M.R., Allsopp, N. & Underhill, L.G., 2016, 'Southern hemisphere biodiversity and global change: data gaps and strategies', *Austral Ecology* 421, 20–30, http://dx.doi.org/10.1111/aec.12391.

Haase, P., Tonkin, J.D., Stoll, S., Burkharde, B., Frenzel, M., Geijzendorffer, I.R., Häuser, C., Klotz, S., Kühn, I., McDowell, W.H., Mirtl, M., Müller, F., Musche, M., Penner, J., Zacharias, S. & Schmeller, D.S., 2018, 'The next generation of site-based long-term ecological monitoring: Linking essential biodiversity variables and ecosystem integrity', *Science of the Total Environment* 613–614, 1376–1384, https://doi.org/10.1016/j.scitotenv.2017.08.111.

Joubert, D.F., Smit, G.N. & Hoffman, M.T., 2013, 'The influence of rainfall, competition and predation on seed production, germination and establishment of an encroaching *Acacia* in an arid Namibian savanna', *Journal of Arid Environments* 91, 7–13, DOI: 10.1016/j.jaridenv.2012.11.001.

Lindenmayer, D.B. & Likens, G.E., 2009, 'Adaptive monitoring – a new paradigm for long-term studies and monitoring', *Trends in Ecology and Evolution* 24, 482–486, DOI: 10.1016/j.tree.2009.03.005.

Lindenmayer, D.B. & Likens, G.E., 2010, 'The science and application of ecological monitoring', *Biological Conservation* 143, 1317–1328, DOI: 10.1016/j.biocon.2010.02.013

Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J. & Watt, A.D., 2010, 'Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time', *Trends in Ecology and Evolution* 25, 574–582, DOI: 10.1016/j.tree.2010.06.016.

Moleele, N.M., Ringrose, S., Matheson, W. & Vanderpost, C., 2002, 'More woody plants? the status of bush encroachment in Botswana's grazing areas', *Journal of Environmental Management* 64, 3–11, DOI: 10.1006/jema.2001.0486.

Moore, A., Van Eck, J.A.J., Van Niekerk, J.P. & Robertson, B.L., 1988, 'Evapotranspirasie in drie plantgemeenskappe van 'n *Rhigozum trichotomum* habitat te Upington', *Journal of the Grassland Society of southern Africa* 5, 80–84, https://doi.org/10.1080/02566702.1988.9648115.

Moustakas, A., Wiegand, K., Getzin, S., Ward, D., Meyer, K.M., Guenther, M. & Mueller, K.-H., 2008, 'Spacing patterns of an *Acacia* tree in the Kalahari over a 61-year period: How clumped becomes regular and *vice versa*', *Acta Oecologica* 33, 355–364, DOI: 10.1016/j.actao.2008.01.008.

Nackley, L.L., Betzelberger, A., Skowno, A., West, A.G., Riley, B.S., Bond, W.J. & Midgley, G.F., 2018. 'CO_2 enrichment does not entirely ameliorate *Vachellia karroo* drought inhibition: A missing mechanism explaining savanna bush encroachment', *Environmental and Experimental Botany* 155, 98–106, DOI: 10.1016/j.envexpbot.2018.06.018.

Parr, T.W., Ferretti, M., Simpson, I.C., Forsius, M. & Kovács-Láng, E., 2002, 'Towards a long-term integrated monitoring programme in Europe: network design in theory and practice', *Environmental Monitoring and Assessment* 78, 253–290, DOI: 10.1023/a:1019934919140.

Peters, D.P.C., Loescher, H.W., SanClements, M.D. & Havstad, K.M., 2014, 'Taking the pulse of a continent: expand-

ing site-based research infrastructure for regional- to continental scale ecology', *Ecosphere* 5, 1–23, http://dx.doi.org/10.1890/ES13-00295.1.

Seymour, C., 2008, 'Grass, rainfall and herbivores as determinants of *Acacia erioloba* (Meyer) recruitment in an African Savanna', *Plant Ecology* 197, 131–138, DOI: 10.1007/s11258-007-9366-x.

Seymour, C. & Milton, S., 2003. '*A collation and overview of research information on* Acacia erioloba *(camelthorn) and identification of relevant research gaps to inform protection of the species*', Department of Water Affairs and Forestry, Pretoria.

Shadwell, E. & February, E., 2017, 'Effects of groundwater abstraction on two keystone tree species in an arid savanna national park', *Peer J* 5, e2923, DOI 10.7717/peerj.2923.

Silvertown, J. & Charlesworth, D., 2001, '*Introduction to plant population biology*', 4th edn., Blackwell Science.

Steenkamp, C.J., Vogel, J.C., Fuls, A., Van Rooyen, N. & Van Rooyen, M.W., 2008, 'Age determination of *Acacia erioloba* trees in the Kalahari', *Journal of Arid Environments* 72, 302–313, DOI: 10.1016/j.jaridenv.2007.07.015.

Tews, J., Schurr, F., Jeltsch, F. & Skarpe, C., 2004, 'Seed dispersal by cattle may cause shrub encroachment of *Grewia flava* on southern Kalahari rangelands', *Applied Vegetation Science* 7, 89–102, DOI: 10.1111/j.1654-109X.2004.tb00599.x.

Van der Merwe, H., Van Rooyen, N., Bezuidenhout, H., Bothma, J. du P. & Van Rooyen, M.W., 2019, '*Vachellia erioloba* dynamics over 38 years in the Kalahari Gemsbok National Park, South Africa', *Koedoe* 61(1), a1534, DOI: 10.4102/koedoe.v61i1.1534.

Van Rooyen, N. & Van Rooyen, M.W., 1998, 'Vegetation of the South-western arid Kalahari: an overview', *Transactions of the Royal Society of South Africa* 53, 113–140, https://doi.org/10.1080/00359199809520381.

Van Rooyen, N., Bredenkamp, G.J., Theron, G.K., Bothma, J du P. & Le Riche, E.A.N., 1994, 'Vegetational gradients around artificial watering points in the Kalahari Gemsbok National Park', *Journal of Arid Environments* 26, 349–361, https://doi.org/10.1006/jare.1994.1037.

Van Rooyen, N., Bezuidenhout, H., Theron, G.K. & Bothma, J du P., 1990. 'Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park, *Koedoe* 33, 63–88, https://doi.org/10.4102/koedoe.v33i1.453.

Van Rooyen, M.W., Van Rooyen, N., Bothma, J. du P. & Van den Berg, H., 2008, 'Landscapes in the Kalahari Gemsbok National Park, South Africa', *Koedoe* 50, 99–112, DOI: 10.4102/koedoe.v50i1.154.
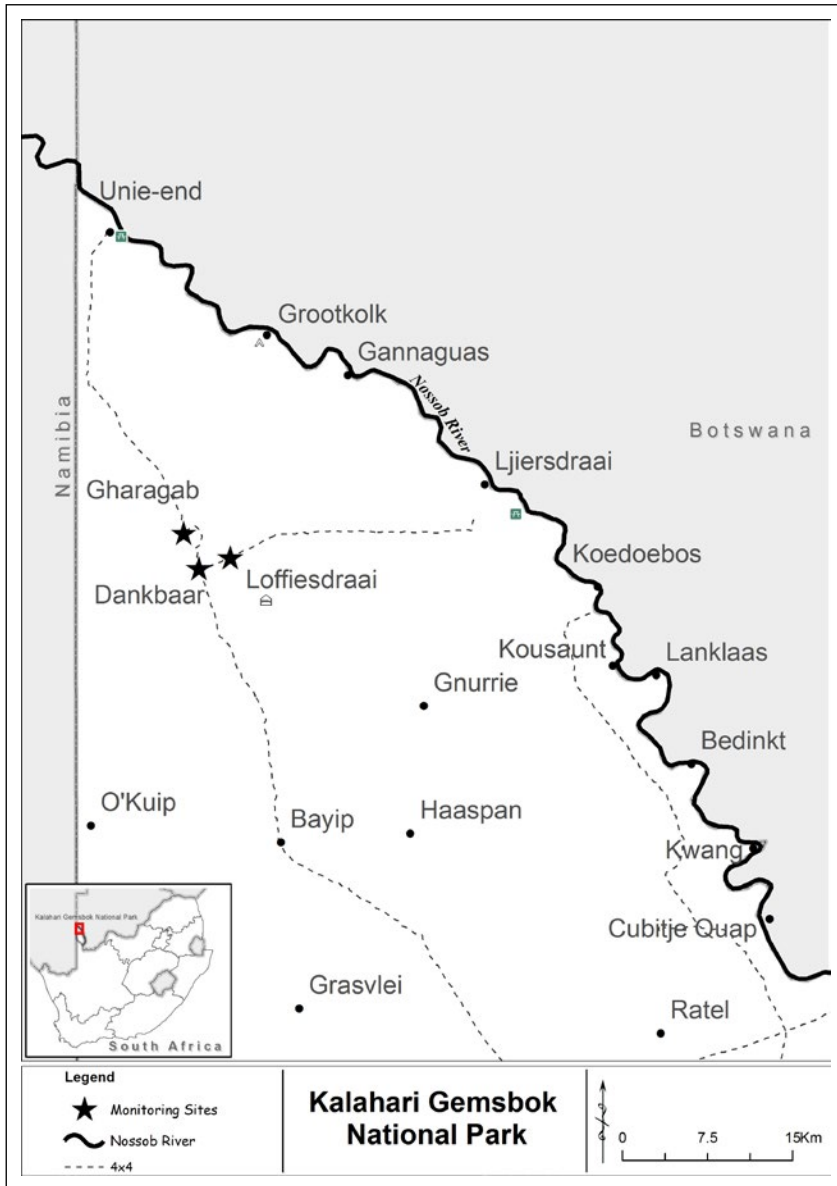
Supplementary Material

FIGURE S1: Location of the Dankbaar artificial watering point and two sites situated 5 km to the north and east of the watering point in the Kalahari Gemsbok National Park.
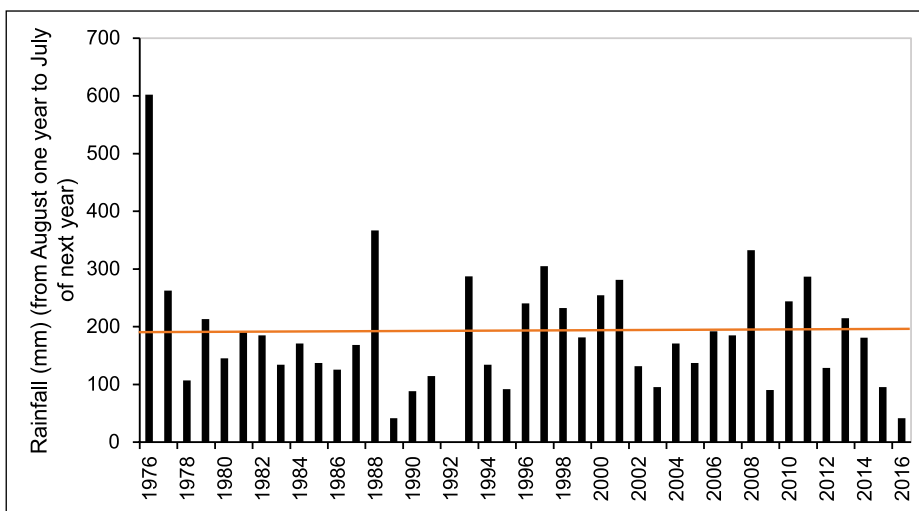

FIGURE S2: Seasonal rainfall (August of one year to July of the next year) at Nossob Rest Camp from 1976 until 2016. Orange line represents the mean annual rainfall of 194 mm (standard deviation ±88.8 mm). Data provided by the South African National Parks.