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Research Article

Structure and composition of *Androstachys johnsonii* woodland across various strata in Gonarezhou National Park, southeast Zimbabwe

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Abstract

A study on the structure and composition of *Androstachys johnsonii* Prain (Euphorbiaceae) woodland across three strata was conducted in Gonarezhou National Park (GNP), southeast Zimbabwe. Specifically, the objectives of the study were: (i) to determine the spatial structure and composition of *A. johnsonii* woodland in GNP and (ii) to determine factors that influence the structure and composition of *A. johnsonii* woodland in GNP. This study was based on a stratified random design with three major soil groups, and 30 plots were sampled in May 2010. The three soil strata were comprised of soils derived from (i) rhyolite, (ii) malvernian and (iii) granophyre bedrocks. A total of 1258 woody plants were assessed and 41 woody species were recorded. There were significant differences in mean tree heights, tree densities, basal area and species diversity in *A. johnsonii* woodland across the three soil strata. In contrast, there were no significant differences in the mean number of dead plants per ha in the three study strata in the GNP. Our study findings suggest that *A. johnsonii* woodland in GNP is being degraded. GNP management should develop a monitoring program through establishing monitoring plots in *A. johnsonii* woodland, and further studies need to be carried out, particularly on recruitment of *A. johnsonii* in the GNP.

Key words: African savanna, elephants, fire damage, Lebombo ironwood, soil group

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Introduction

Savanna systems are characterized by a mixture of trees and grasses where the relative dominance of woody cover is determined by biotic and abiotic factors [1]. Savannas occupy a fifth of the earth's land surface and support a large proportion of the world's human population and most of its rangeland, livestock and wild herbivore biomass [1]. *Androstachys johnsonii* Prain (Euphorbiaceae), the Lebombo ironwood, is an evergreen tree with a maximum height of about 15 m [2]. The evergreen *A. johnsonii* canopy remains green throughout the year and provides important forage and shade for wildlife at a time when many other trees are leafless.

High population densities of about 1.8 elephants per km² of African elephants (*Loxodonta africana*) and high fire frequencies in Gonarezhou National Park (GNP), southeast Zimbabwe, are likely to be the major factors perpetuating the loss of *A. johnsonii* woodland. This may lead to a shift from savanna woodland to scrubland or grassland [3] and might pose problems to wildlife management in GNP. The decline of *A. johnsonii* woodland where wildlife concentrates during the dry season has been of concern to the wildlife managers in GNP. Changes in woody vegetation structure and composition may have important implications for wildlife habitat, biotic diversity and risk of future disturbances [4].

Previous studies in GNP, southeast Zimbabwe, suggest that fire is an important factor that has contributed to woodland stand dynamics. Tafangenyasha [5] reported that frequent fires in GNP led to the decline of canopy woodlands and herbaceous plant cover. In addition, Tafangenyasha [6] suggested that fire and elephant herbivory contributed to the general modification of habitats and, in particular, to the decline of *Brachystegia glaucescens* woodland in GNP. *Androstachys johnsonii* is of restricted distribution and is a relatively rare species in Zimbabwe. The woodland is vulnerable to elephant and fire damage during the dry season.

Successful management of large areas of natural vegetation depends to a large measure on knowledge of vegetation composition, the extent to which the vegetation is used, and changes which take place in response to fire and other disturbances [7]. Therefore, the aim of the present study was to determine the structure and composition of *A. johnsonii* woodland, and to contribute towards woodland restoration strategies in GNP. Specifically, the objectives of the study were: (i) to determine the spatial structure and composition of *A. johnsonii* woodland in GNP and (ii) to determine factors that influence the structure and composition of *A. johnsonii* woodland in GNP.

Methods

Study areas

Established in the early 1930s as a Game Reserve, GNP was transformed into a national park under the Parks and Wildlife Act of 1975. GNP has been part of the Great Limpopo Transfrontier Park since 2000. Covering an area of 5053 km², GNP is located in the southeast lowveld of Zimbabwe, between 21° 00'–22° 15' S and 30° 15'–32° 30' E (Fig. 1). GNP experiences two seasons, a wet season and a dry season, which are contrasting. Annual average rainfall is about 466 mm, with October to March being the wettest months. The dry season normally lasts from April to September. Average monthly maximum temperatures are 25.9 °C in July and 36 °C in January. Average monthly minimum temperatures range between 9 °C in June and 24 °C in January [3].

The major vegetation type is *Colophospermum mopane* woodland, which covers approximately 40% of GNP. There is a wide variety of large herbivore species in the GNP ecosystem, including African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), waterbuck (*Kobus ellipsiprymnus*), roan antelope (*Hippotragus equinus*), sable (*Hippotragus niger*), Burchell's zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), African elephant and hippopotamus (*Hippopotamus amphibius*). The park has a number of large carnivores such as lion (*Panthera leo*) and spotted hyena (*Crocuta*

crocuta) [8].

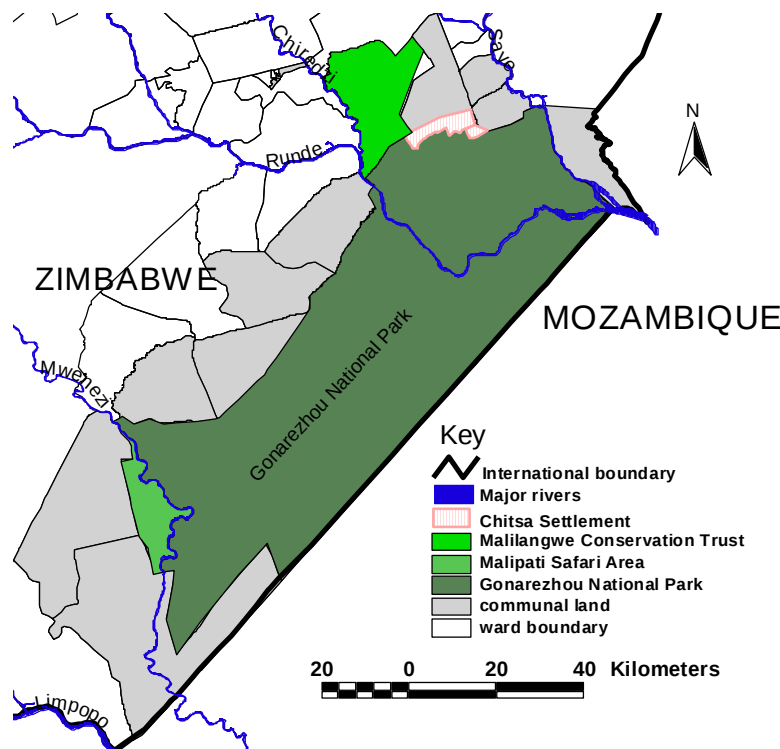


Fig. 1. Location of the Gonarezhou National Park (GNP) in southeast Zimbabwe.

Experimental layout and selection of sampling plots

This study was based on a stratified random design [9] on three different soil groups. Accordingly, the position of the plots followed stratification according to three soil groups namely, (i) rhyolite, (ii) malvernian and (iii) granophyre bedrock derived soils [10]. For each of the three soil groups, 10 replicate plots were randomly placed in *A. johnsonii* woodland patches. All *A. johnsonii* woodland patches in GNP were selected from the vegetation map of Sherry [11]. Sampling plots within the woodland were located by generating random points (Global Positioning System [GPS] coordinates) in the selected *A. johnsonii* woodland patches on a vegetation map in Arc View 3.2 software package. Guided by a GNP topographical map, GPS handsets were used to track the position of the plots across the woodland.

Data collection

For the purpose of this study, sampling plots measuring 20 × 50 m were used. This plot size satisfies the consideration by Walker [7] of including at least 15-20 trees of the most important study species in a plot. Trees were defined as rooted, woody, self-supporting plants ≥3m high with a basal stem diameter ≥6cm, whereas shrubs were defined as rooted, self supporting <3m high and <6cm in stem basal diameter [3,12]. All woody plants rooted within the plot were recorded and measured. Woody plants occurring along plot margins were included if at least half of the rooted system was inside the plot [7]. For multi-stemmed plants located at edges of plots, only stems with more than half their base inside the plot were measured. The floristic composition and structure of the woody vegetation component were assessed at the end of the rainy season, i.e. in May 2010, when species composition was best represented [7].

All woody plant species were identified using a field guide by Coates-Pelgrave [2]. The height of woody vegetation was measured by placing a calibrated 6 m pole against a tree. For trees >6 m, the pole was manually uplifted or height visually estimated by observing it at a distance away from the tree. For multi-stemmed plants, only the height of the tallest stem was considered. The basal circumference of each stem was measured just above the buttress swelling, to the nearest centimeter, using a flexible 5 m tape measure. Every woody component in the plot was assessed for elephant and fire damage. Elephant damage was associated with broken stems and branches, bark stripping, scarring, uprooted or felled trees [12]. Fire damage indicators were fire scars, scorch marks on branches, dead, burnt stems and charred plant remains [3]. All woody plants were assessed to establish whether they were dead or alive. Because we conducted our field study towards the end of the rainy season, dead plants were denoted as plants without living leaves, with dry and cracking trunks, barks and stems.

Data Analyses

Variables included in the analyses were woody plant height, basal area, density and species diversity. Data were tested for normality using the Kolmogorov-Smirnov test in STATISTICA version 6 package [13] and all data were found to be normal. Descriptive statistics (means and standard errors) were calculated for all vegetation variables. Plant densities for each plot were converted into per hectare (ha). The Shannon Index (H') was calculated using the formula: $H' = - \sum (pi) \times \text{LN}(pi)$, where pi is the proportional abundance of a species and LN is the natural logarithm [14].

A One-Way ANOVA using STATISTICA statistical software with strata as categorical predictors and vegetation variables as dependent variables was performed to test the main effects of variables and strata (P -value at 0.05 significance level). For variables with significant differences, differences among means were tested using the Fisher Least Significant Difference (LSD) post-hoc tests to detect differences between the three soil categories. Data were further analyzed through a combination of classification and ordination techniques to explore the associations, patterns and structure of woody vegetation across the three strata. A Principal Component Analysis (PCA) was used to define both the pattern and structure of variables [15] in the different strata using the vegetation variables. Hierarchical Cluster Analysis (HCA) using the weighted pair group average linkage method was performed using a matrix of 30 plots and 41 species, using the species abundance data to classify sampling plots on the basis of their floristic similarity.

Results

Woody species composition and abundance

A total of 1258 woody plants (shrubs and trees) were assessed in 30 sampling plots, and 41 woody species were recorded. About 68% of the woody plants were living trees, 32% were dead stems, 43% showed evidence of elephant damage and 58% of the sampled woody components showed evidence of fire damage. *Androstachys johnsonii* was the dominant woody species and at most times was found in pure stands (Fig. 2).



Fig. 2. *Androstachys johnsonii* woodland in Gonarezhou National Park (GNP), southeast Zimbabwe. Photos: P. Zisadza-Gandiwa.

Androstachys johnsonii woody vegetation structure and composition across the three strata in GNP

First, there were significant differences in tree heights in *A. johnsonii* woodland across the three strata. Plots in granophyre derived soils had the highest tree heights compared to the other two strata (Table 1). Secondly, there were significant differences in tree density in *A. johnsonii* woodland across the three strata. Plots in granophyre derived soils had the highest tree density compared to the other two strata. Thirdly, in contrast, there were no significant differences in the density of dead plants across the three strata in the GNP. Fourthly, there were significant differences in basal areas in *A. johnsonii* woodland across the three strata. Plots in the rhyolite derived soils had the highest basal areas compared to the other two strata. Lastly, there were significant differences in species diversity in *A. johnsonii* woodland across the three strata. Plots in the rhyolite derived soils had the greatest diversity compared to the other two strata. *Androstachys johnsonii*, *C. mopane*, *Combretum apiculatum* and a few other species in *A. johnsonii* woodland showed higher propensity to coppice in all disturbed sites. High coppicing was evidence of elephant and fire disturbance. Coppicing varied amongst species. However, we observed few seedlings of *A. johnsonii* in all sampling plots.

Table 1. Attributes of woody vegetation structure and composition for plots in *Androstachys johnsonii* woodland in Gonarezhou National Park (GNP), southeast Zimbabwe (Mean and Standard Error, SE). n = 10 plots/strata. Mean values with different superscript letters within rows differ significantly (LSD; $P < 0.05$)

	Strata						
	Rhyolite derived soils		Malvernian bed derived soils		Granophyre derived soils		
Variable	Mean	SE	Mean	SE	Mean	SE	Significance: One-way ANOVA
Height (m)	3.55 ^a	0.34	3.89 ^a	0.33	9.19 ^b	0.53	$F_{2,27} = 58.67$; $P < 0.001$
Tree density (ha)	648.33 ^a	54.12	555.00 ^a	39.44	893.33 ^b	45.22	$F_{2,27} = 14.03$; $P < 0.001$
Dead trees density (ha)	216.67 ^a	26.30	201.67 ^a	24.27	220.00 ^a	53.56	$F_{2,27} = 0.069$; $P = 0.933$
Basal area (m)	4.10 ^a	0.72	1.96 ^b	0.16	2.56 ^b	0.25	$F_{2,27} = 5.980$; $P = 0.007$
Species diversity (H')	0.96 ^a	0.14	0.24 ^b	0.11	0.28 ^b	0.09	$F_{2,27} = 11.93$; $P < 0.001$

Structure and pattern of A. johnsonii woodland in GNP

Principal Components Analysis (PCA) output of 5 vegetation variables shows Factor 1 accounting for 41.35% and Factor 2 accounting for 23.07% of the variance (Fig. 3). Tree height and basal area were negatively correlated to Factor 1 whilst density of woody plants and dead plants were positively correlated to Factor 1. Factor 1 therefore defines a gradient from taller trees with a higher basal area to areas with higher density. Factor 2 defines a gradient from areas with higher species diversity to areas with higher density of dead plants. Consequently, plots with taller trees and higher basal areas scored low on Factor 1, mostly sample plots falling in the rhyolite derived soils, whereas those with a higher density of woody plants scored high on Factor 1, mostly sample plots from the granophyre derived soils. Sample plots with higher species diversity scored low on Factor 2, mostly plots from the malvernian bed derived soils. Overall, the majority of sample plots in *A. johnsonii* woodland in all the strata were characterized by higher numbers of dead plants and higher basal areas.

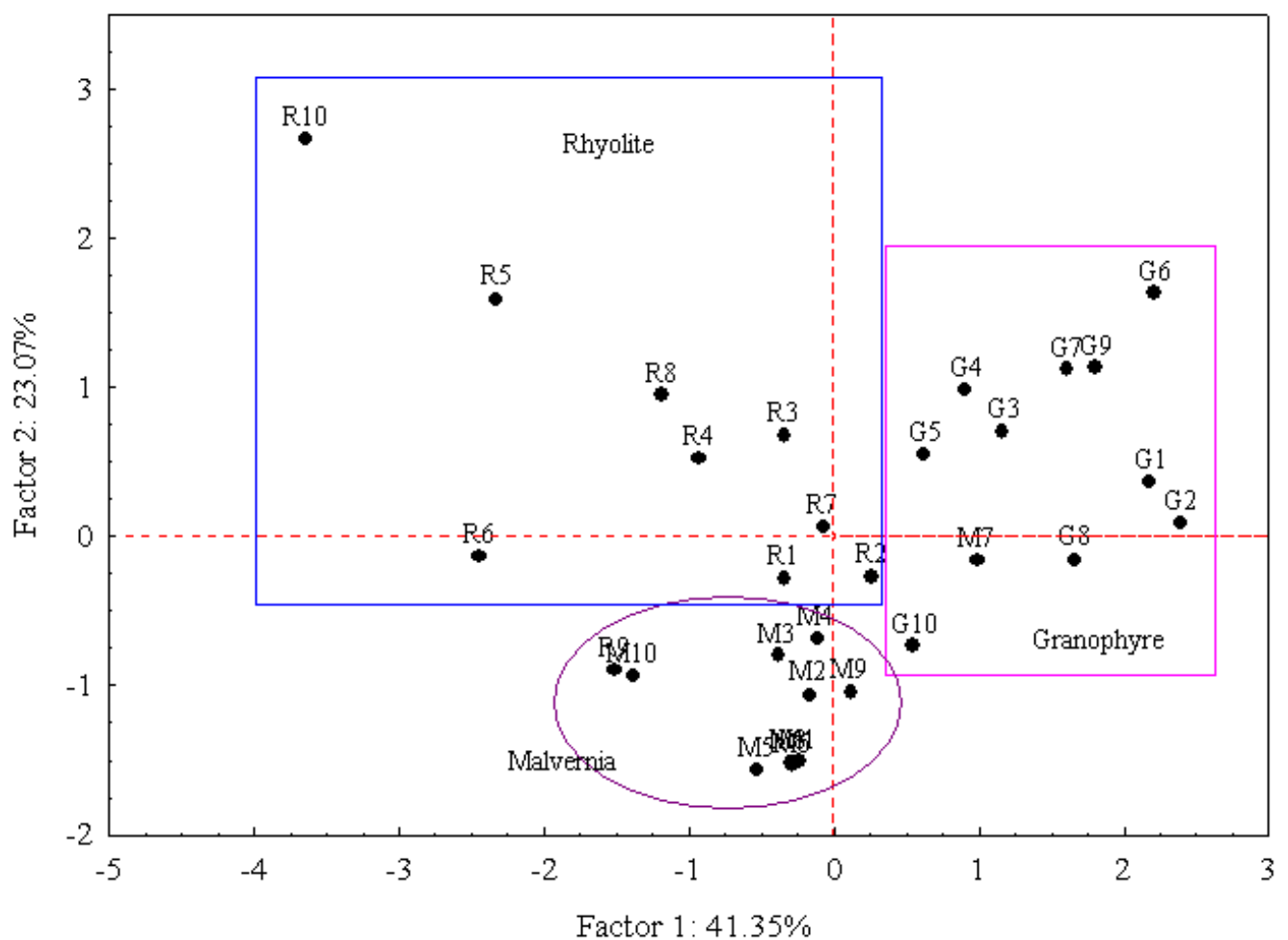


Fig. 3. Principal Component Analysis (PCA) scatter plot of 30 sample plots in *Androstachys johnsonii* woodland in Gonarezhou National Park (GNP), southeast Zimbabwe. Notes: R-denotes sample plots from the Rhyolite derived soils; M-denotes sample plots from Malvernian bed derived soils and G-denotes sample plots from Granophyre derived soils.

Species association in A. johnsonii woodland in GNP in relation to the three study strata

The Hierarchical Cluster Analysis (HCA) dendrogram showed three broad clusters from the 30 sampled plots in *A. johnsonii* woodland in GNP (Fig. 4). Cluster A had only sample plots drawn from granophyre derived soil strata. Plots in Cluster A were characterized by an association of the following species: *A. johnsonii*, *C. mopane*, *Spirostachys africana*, *Xeroderris stuhlmannii*, *Terminalia prunioides* and *Grewia bicolor*. Cluster B comprised sample plots from both rhyolite and malvernian bed derived soil groups in *A. johnsonii* woodland and included the following common woody species: *A. johnsonii*, *C. apiculatum*, *Combretum celastroides*, *Boscia angustifolia*, *Canthium* spp., *Alchornea laxiflora* and *Phyllanthus reticulatus*. Lastly, Cluster C comprised a mixture of plots from all the three study soil groups in GNP and consisted of diverse species composition.

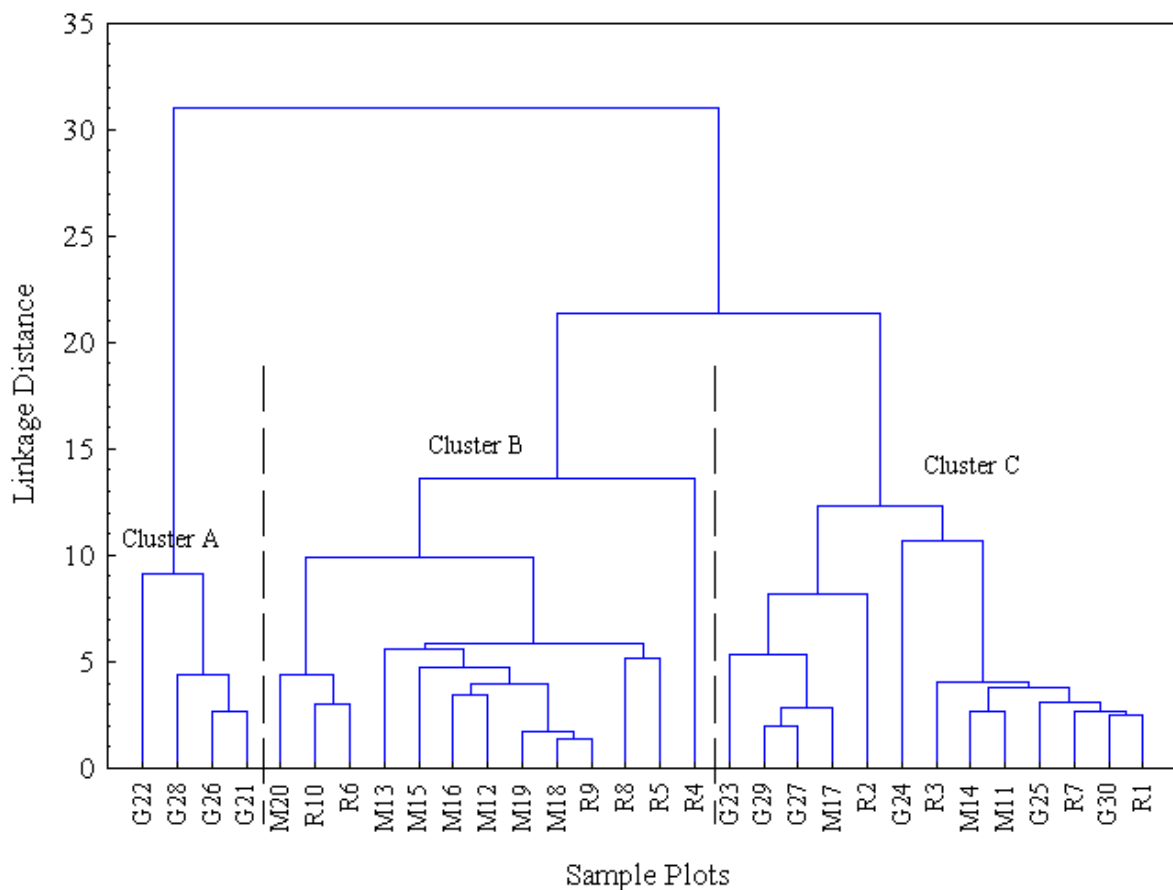


Fig. 4. Hierarchical Cluster Analysis (HCA) dendrogram showing classification of sample plots into three (3) clusters based on species abundance data from the 30 sample plots in *Androstachys johnsonii* woodland in Gonarezhou National Park (GNP), southeast Zimbabwe. Notes: R-denotes sample plots from the Rhyolite derived soils; M-denotes sample plots from Malvernian bed derived soils and G-denotes sample plots from Granophyre derived soils.

Discussion

This study recorded significant differences in height, basal area, tree density and species diversity of *A. johnsonii* woodland in GNP. The structural and compositional differences in *A. johnsonii* woodland in GNP probably result from factors such as herbivory, fires, soil differences, soil moisture, past human activities and droughts. *Androstachys johnsonii* woodland in the northern section of GNP, an area with high fire frequency and high elephant density, seems to be degraded. The reduced heights in woody species show that elephants and fire are influencing the woodland. Repeated fires are known to stress normal growth and affect the health of the woodland, while elephant browsing may top-kill woody species [3]; hence *A. johnsonii* species fail to grow to their maximum attainable height of about 15 m [2]. It was evident from this study that *A. johnsonii* trees occurring in all the three soil strata were to some extent damaged by elephants and showed evidence of past fires in GNP. There was noticeable damage to *A. johnsonii* woodland in areas of high elephant density and frequent fires [3]. Tree damage was not uniform, however. Larger trees were less damaged by elephants and fire. In contrast, most damage was recorded on the juveniles and immature trees. Affected trees showed burn marks, scars, black surfaces and charred plant remains. Elephant damage was characterized by breaking of branches and stems, uprooting, pushing over and scarring of woody species. However, trees on hilltops and rocky outcrops showed evidence of slight elephant damage, whereas trees in the plains were more damaged by elephants. This may be attributed to difficult access by elephants to hilltops and rocky outcrops. One of the major reasons why elephants target *A. johnsonii* trees can be attributed to their evergreen nature. This is compounded by the social behaviour of elephants, including indiscriminate destruction of trees, especially by the male groups [16]. In areas with high elephant densities, vegetation is destroyed not only by browsing but also by trampling. It has been suggested that some of the tree felling may be a social display unrelated to feeding [17]. Additionally, elephants often change the structure and composition of vegetation, particularly in areas close to water sources [12]. In semi-arid savannas, a clear example of spatial heterogeneity in environmental impact by herbivores is the development of utilization gradients around water sources where the grazing and trampling are high [18].

Androstachys johnsonii trees showed evidence of resprouting from the base after being pushed by elephants and also after being burnt. Disturbance, such as herbivory and repeated fires in the study area, likely promoted vigorous resprouting of *A. johnsonii*. This is an important observation, as it is likely to modify and influence state-and-transition dynamics in *A. johnsonii* woodland, thus affecting the resultant population structure. Additionally, there was evidence of large tree mortality, most likely from past droughts, elephants and fire damage in GNP, as represented by moderate dead tree densities and evidence of resprouting or coppicing observed in the current study. Observed differences in coppice in *A. johnsonii* woodland may be attributed to the inherent properties of each tree species in the face of herbivory and fire damage. The observed low seedling density of *A. johnsonii* woodland in this present study could be a result of repeated browsing by herbivores and fires in GNP, resulting in insufficient time for the trees to recover from the disturbances. It has been demonstrated that browsing by herbivores reduces woody seedling survival substantially in savanna ecosystems [19]. In the neighbouring Kruger National Park and bordering areas, South Africa, there is growing evidence that many plant species resprout from the base after fire or when elephants push trees over [20-22]. Similarly, resprouting has been reported in human-dominated savanna woodlands where trees of various sizes are cut down for various uses [23-25].

Several other studies of savanna ecosystems have reported that fire and elephants influence savanna woodland structure and composition. For example, earlier studies in GNP have shown that fire and elephants are major drivers of woodland changes [3,26,27]. The population density of elephants is gradually increasing in GNP [28], and the population increase may result in woodland destruction. We observed that past droughts have contributed mostly to the death of *A. johnsonii* trees as opposed to other tree species in GNP. Droughts have been suggested as also influencing tree loss and

habitat changes in GNP [5]. Further, Tafangenyasha [6] concluded that fire and elephant damage were powerful factors leading to loss of woodlands like *B. glaucescens* woodland in GNP. Elsewhere, earlier studies by Ben-Shahar [12], Guy [29] and Heintz [30] also attest to fire and elephants being major ecosystem engineers in the savanna ecosystem. Fire and herbivory are the key determinants of the savanna ecosystems [31]. The synergistic relationship between fire and herbivory is the main cause of spatial heterogeneity of habitats and ecosystems [32].

The destructive behaviour by elephants increases tree mortality and may result in conversion of woodland to grassland [33]. For example, in GNP some *A. johnsonii* woodlands are degraded as a result of elephant browsing (Fig. 5). Pruning by large herbivores strongly influences sapling morphology and recruitment to adult size [34]. Recruitment is controlled by rainfall, which limits seedling establishment, and fire, which prevents recruitment into adult-size classes [35]. In addition, browsing herbivores can indirectly decrease seedling establishment by drastically reducing tree reproductive output [36]. However, it has been suggested that in some cases large mammals may indirectly increase seedling survival of some tree species and accelerate, rather than inhibit, tree recruitment [37]. Additionally, savanna woody plants have evolved with disturbances such as fire and herbivory and hence have traits to resist or tolerate both these disturbances [38].



Fig. 5. Images of elephant damaged *Androstachys johnsonii* trees (left) and elephants (right) in Gonarezhou National Park (GNP), southeast Zimbabwe. Photos: P. Zisadza-Gandiwa

The present study shows that species diversity was higher in areas with high disturbance such as areas with high fire frequencies and elephant densities [3,28]. These results are in line with earlier studies in the Southern African savanna ecosystem [39-43]. High species composition in areas of high disturbance can be attributed to the fact that frequent fires destroy trees and create gaps that serve as niches for invasion by other species. This is supported by the theory of invasibility, which states that whenever there are unutilized resources in an ecosystem following disturbance, that ecosystem becomes susceptible to invasion [44]. A reduction in species diversity in less frequently disturbed areas can be attributed to competition for resources and dominance by a single species. For example, *A. johnsonii* species are characterized by forming dense thickets that dominate other species.

Implications for conservation

Management

This study has shown that *A. johnsonii* woodland in GNP is being transformed into low-density and shorter woodland. Overall, the significant structural differences in *A. johnsonii* woodland can be attributed to herbivory, droughts and fires, whereas the significant variation in composition of *A. johnsonii* woodland in different study plots can be attributed to differences in underlying geology

(edaphic) and biotic factors. Structural changes in savannas have consequences for management because of their effects on herbage quantity, composition and nutrient dynamics [45]. Therefore, we suggest the following: first, long-term monitoring in woodland composition and structure is necessary in order to determine possible changes over time and appropriate management practices, which include the maintenance of biodiversity and ecosystem rehabilitation. Knowledge of the state and dynamics of the woodlands is required to achieve a sustainable use of these resources [46]. Hence, woodland composition and structure are some of the elements that should be addressed through establishing long-term monitoring plots in GNP. Second, there is need for further studies on *A. johnsonii* woodland in GNP. Future studies in GNP should focus on generating detailed information on the regeneration, resprouting and response of *A. johnsonii* to various forms of disturbance.

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References

- [1] Scholes, R.J. and Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517-544.
- [2] Coates-Pelgrave, K. 1997. *Trees of Southern Africa*. Struik Publishers, Cape Town.
- [3] Gandiwa, E. and Kativu, S. 2009. Influence of fire frequency on *Colophospermum mopane* and *Combretum apiculatum* woodland structure and composition in northern Gonarezhou National Park, Zimbabwe. *Koedoe*: 51(1), Art. #685, 13 p, DOI: 10.4102/koedoe, v51i1.685.
- [4] Peterson, D.W. and Reich, P.B. 2001. Prescribed fire in Oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications* 11(3): 914-927.
- [5] Tafangenyasha, C. 1997. Tree loss in Gonarezhou National Park (Zimbabwe) between 1970 and 1983. *Journal of Environmental Management* 49: 355-366.
- [6] Tafangenyasha, C. 2001. Decline of the mountain acacia, *Brachystegia glaucescens* in Gonarezhou National Park, Southeast Zimbabwe. *Journal of Environmental Management* 63: 37-50.
- [7] Walker, B.H. 1976. An approach to the monitoring of changes in the composition and utilisation of woodland and savanna vegetation. *South African Journal of Wildlife Research* 6(1): 1-32.
- [8] Zisadza, P., Gandiwa, E., Van Der Westhuizen, H., Van Der Westhuizen, E. and Bodzo, V. 2010. Abundance, distribution, and population trends of hippopotamus in Gonarezhou National Park, Zimbabwe. *South African Journal of Wildlife Research* 40(2): 149-157.
- [9] Mueller-Dombois, D. and Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. John Wiley and Sons, New York.
- [10] Tafangenyasha, C. 1992. *Provisional map and description of surface geology of Gonarezhou National Park*. Unpublished report. Department of National Parks and Wildlife Management, Harare.
- [11] Sherry, B.Y. 1977. *Basic vegetation types of the Gonarezhou National Park, Zimbabwe*. Project No. GNP/3Y/2. Department National Parks and Wildlife Management, Harare.

- [12] Ben-Shahar, R. 1998. Changes in structure of savanna woodlands in northern Botswana following the impacts of elephant and fire. *Plant Ecology* 136: 189-194.
- [13] StatSoft, Inc. 2001. *STATISTICA version 6*, Tulsa.
- [14] Ludwig, A.J. and Reynolds, J.F. 1988. *Statistical Ecology. A Primer on Methods and Computing*. John Wiley and Sons, New York.
- [15] McGarigal, K., Cushman, S. and Stafford, S. 2000. *Multivariate statistics for wildlife and ecology research*. Springer-Verlag, New York.
- [16] Hofmeyr, M. and Eckardt, H. 2006. *Elephant effects on vegetation*. Center for African Ecology, University of Witwatersrand, Johannesburg.
- [17] Midgley, J.J., Balfour, D. and Kerley, G.I.H. 2005. Why do elephants damage savanna trees? *South African Journal of Science* 101: 213-215.
- [18] Chamaille-James, S., Valeix, M. and Fritz, H. 2007. Managing heterogeneity in elephant distribution: interactions between elephant population, density and surface water available. *Journal of Applied Ecology* 4: 24-30.
- [19] Moe, S.R., Rutina, L.P., Hytteborn, H. and Du Toit, J.T. 2009. What controls woodland regeneration after elephants have killed the big trees? *Journal of Applied Ecology* 46: 223-230.
- [20] Neke, K.S., Owen-Smith, N. and Witkowski, E.T.F. 2006. Comparative resprouting response of savanna woody plant species following harvesting: the value of persistence. *Forest Ecology and Management* 232: 114-123.
- [21] Helm, C.V., Witkowski E.T.F., Kruger L., Hofmeyr, M. and Owen-Smith, N. 2009. Mortality and utilisation of *Sclerocarya birrea* subsp. *caffra* between 2001 and 2008 in the Kruger National Park, South Africa. *South African Journal of Botany* 75: 475-84.
- [22] Helm, C.V., Scott, S.L. and Witkowski, E.T.F. 2011. Reproductive potential and seed fate of *Sclerocarya birrea* subsp. *caffra* (marula) in the low altitude savannas of South Africa. *South African Journal of Botany*. DOI:10.1016/j.sajb.2011.02.003
- [23] Luonga, E.J., Witkowski, E.T.F. and Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 164: 15-30.
- [24] Luoga, E.J., Witkowski, E.T.F. and Balkwill, K. 2004. Regeneration by coppicing (resprouting) of Miombo (African savanna) trees in relation to land use. *Forest Ecology and Management* 189: 23-35.
- [25] Chinuwo, T., Gandiwa, E., Mugabe, P.H., Mpofu, I.D.T. and Timpong-Jones, E. 2010. Effects of previous cultivation on regeneration of *Julbernardia globiflora* and *Brachystegia spiciformis* in grazing areas of Mupfurdzi Resettlement Scheme, Zimbabwe. *African Journal of Range & Forage Science* 27(1): 45-49.
- [26] Tafangenyasha, C. 1998. Phenology and mortality of common woody plants during and after severe drought in south-eastern Zimbabwe. *Transactions of the Zimbabwe Scientific Association* 72: 1-6.
- [27] Gandiwa, E., Magwati, T., Zisadza, P., Chinuwo, T. and Tafangenyasha, C. 2011. The impact of African elephants on *Acacia tortilis* woodland in northern Gonarezhou National Park, Zimbabwe. *Journal of Arid Environments*. DOI:10.1016/j.jaridenv.2011.04.017
- [28] Dunham, K.M., Van Der Westhuizen, E., Van Der Westhuizen, H.F. and Gandiwa, E. 2010. *Aerial survey of elephants and other large herbivores in Gonarezhou National Park, (Zimbabwe), Zinave National Park (Mozambique) and surrounds: 2009*. Zimbabwe Parks and Wildlife Management Authority, Harare.
- [29] Guy, Y. 1989. The feeding behaviour of elephants (*Loxodonta africana*) in the Sengwe area Rhodesia. *South African Journal of Wildlife* 6(1): 55-63.
- [30] Heint, M. 2005. *Fire regime and vegetation response in the Okavango Delta, Botswana*. PhD Dissertation. Technische Universität München, Freising-Weihenstephan, Germany.
- [31] Tainton, N.M. Ed. 1998. *Veld management in Southern Africa*. University of Natal Press, Pietermaritzburg.

- [32] Mapaure, I. and Campbell, B.M. 2002. Changes in miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. *African Journal in Ecology* 40: 212-219.
- [33] Van De Koppel, J. and Prins, H.H.T. 1998. The importance of herbivore interactions for the dynamics of African savanna woodlands: An hypothesis. *Journal of Tropical Ecology* 14(5): 565-576.
- [34] Fornara, D.A. and Du Toit, J.T. 2008. Responses of woody saplings exposed to chronic mammalian herbivory in an African savanna. *Ecoscience* 15(1): 129-135.
- [35] Higgins, S.I., Bond, W.J. and Trollope, W.S.W. 2000. Fire, resprouting and variability: A recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88(2): 213-229.
- [36] Fornara, D.A. and Du Toit, J.T. 2007. Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology* 88: 200-209.
- [37] Goheen, J.R., Keesing, F., Allan, B.F., Ogada, D. and Ostfeld, R.S. 2004. Net effects of large mammals on *Acacia* seedling survival in an African Savanna. *Ecology* 85(6): 1555-1561.
- [38] Helm, C., Wilson, G., Midgley, J., Kruger, L. and Witkowski, E.T.F. 2011. Investigating the vulnerability of an African savanna tree (*Sclerocarya birrea* ssp. *caffra*) to fire and herbivory. *Austral Ecology*. DOI: 10.1111/j.1442-9993.2010.02232.x
- [39] Booysen, P.D.V. and Tainton, N.M. 1984. *Ecological effects of fire in South African ecosystems*. Ecological Studies 48 Springer-Verlag, Berlin.
- [40] Childes, S.L. and Walker, B.H. 1987. Ecology and dynamics of the woody vegetation on the Kalahari sands in Hwange National Park, Zimbabwe. *Vegetatio* 72: 111-128.
- [41] Holdo, R.M. 2007. Elephants, fire and frost can determine community structure and composition in Kalahari woodlands. *Ecological applications* 17(2): 558-568.
- [42] Sabiiti, E.N. and Wein, R.W. 1988. Fire behaviour and the invasion of *Acacia sieberiana* into savanna grassland openings. *African Journal of Ecology* 26: 301-313.
- [43] Shackleton, C.M. and Scholes, R.J. 2000. Impact of fire frequency on woody community structure and soil nutrients in Kruger National Park. *Koedoe* 43(1): 75-81.
- [44] Davis, M.A., Grime, J.P. and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528-534.
- [45] Fensham, R.J. and Holman, J.E. 1999. Temporal and spatial patterns in drought-related tree dieback in Australian savanna. *Journal of Applied Ecology* 36: 1035-1050.
- [46] Dharani, N., Kinyamario, J.I. and Onyari, J.M. 2006. Structure and composition of *Acacia xanthophloea* woodland in Lake Nakuru National Park, Kenya. *African Journal of Ecology* 44: 523-530.