

International Journal of Biodiversity and Conservation Vol. 5(2), pp. 71-77, February, 2013

Available online <http://www.academicjournals.org/IJBC>

DOI: 10.5897/IJBC12.095

ISSN 2141-243X ©2013 Academic Journals

Full Length Research Paper

Variation in woody vegetation structure and composition in a semi-arid savanna of Southern Zimbabwe

Patience Zisadza-Gandiwa¹, Lovemore Mango², Edson Gandiwa^{1,3*}, David Goza⁴, Chenjerai Parakasingwa¹, Exeverino Chinoitezvi⁴, Julius Shimbani¹ and Justice Muvengwi²

¹Scientific Services, Gonarezhou National Park, Parks and Wildlife Management Authority, Private Bag 7003, Chiredzi, Zimbabwe.

²Department of Environmental Sciences, Bindura University of Science Education, Private Bag 1020, Bindura, Zimbabwe.

³Resource Ecology Group, Wageningen University, P.O. Box 47, 6700 AA, Wageningen, The Netherlands.

⁴Mushandike College of Wildlife Management, Parks and Wildlife Management Authority, Private Bag 9036, Masvingo, Zimbabwe.

Accepted 24 January, 2013

The objectives of this study were: i) to establish the status of woody vegetation structure and composition, and ii) to determine the main factors influencing woody vegetation structure and composition across Gonarezhou National Park, Zimbabwe. We divided the park into three large strata based on natural and artificial features. A total of 137 sample plots were randomly placed to gather data on woody vegetation in the three study strata across Gonarezhou National Park from May to June 2011. Trees constituted 66% and shrubs 34% of the woody plants sampled. A total of 132 woody plant species were recorded. Significant differences were found in basal area, shrub density, browsed plants density and woody species diversity across Gonarezhou National Park. In contrast, no significant differences were recorded in tree height, densities of trees, stems, dead plants and fire damaged plants. Our results suggest that there are some variations in woody vegetation structure and composition across Gonarezhou National Park. These variations could be attributed to both natural and anthropogenic disturbance factors including elephant (*Loxodonta africana* Blumenbach) browsing, fires, droughts and previous tsetse fly (*Glossina* spp.) (Diptera: Glossinidae) eradication activities in the park.

Key words: Elephants, fire, Gonarezhou National Park, savannas, woody vegetation.

INTRODUCTION

Savannas are one of the world's most extensive biomes (Williams et al., 1996). They comprise systems with a continuous herbaceous layer and a discontinuous woody stratum (Scholes and Archer, 1997; Sankaran et al., 2008). Accordingly, woody vegetation structure and composition plays important roles in the functioning of

ecosystems and service provision. However, the structure and composition of woody vegetation in savannas is thought to be influenced by water availability, nutrient availability, fire and herbivory typology and grazing pressure (Frost et al., 1986). Moreover, human activities also influence the structure and composition of woody vegetation in savanna ecosystems (Skarpe, 1990). The loss of woody vegetation due to herbivory, fires, drought, frost, diseases and human disturbances is a cause for concern and it has been an area of continuous research focus (example Ben-Shahar, 1998;

*Corresponding author. E-mail: egandiwa@gmail.com. Tel: +263 773 490 202.

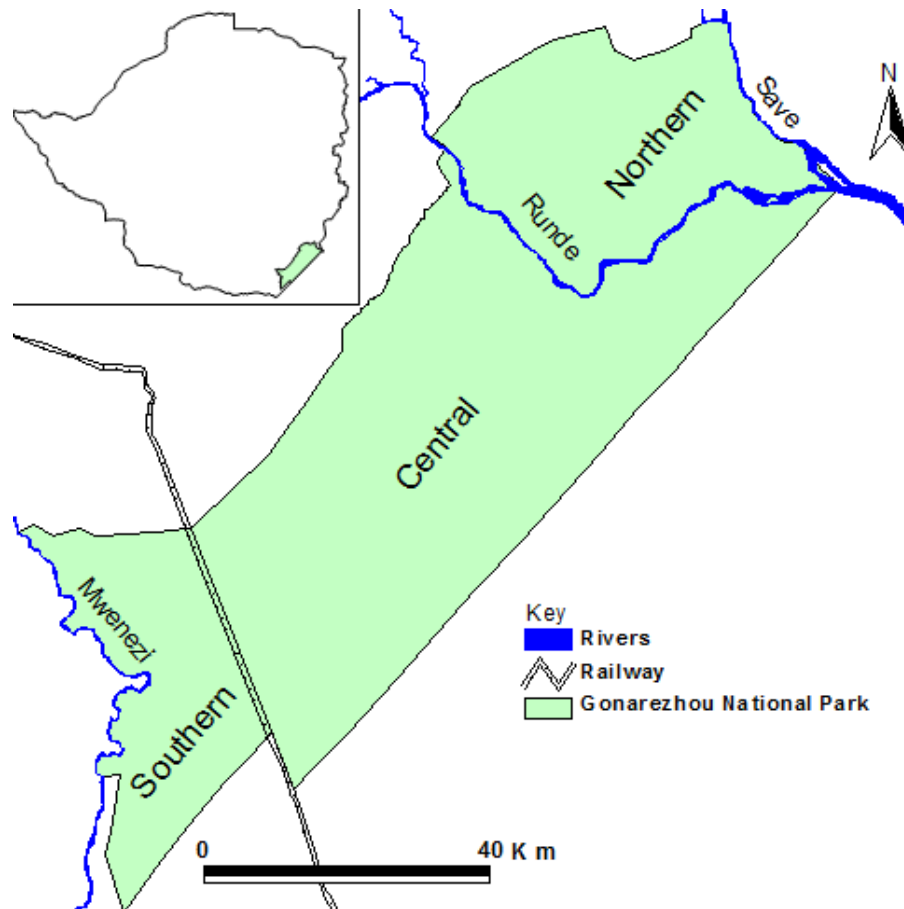


Figure 1. Location of the three study strata in Gonarezhou National Park, southern Zimbabwe.

Tafangenyasha, 1998; Holdo, 2007; Alamu and Agbeja, 2011; O'Kane et al., 2012). For instance, there has been an increasing concern over the detrimental effects of localized African elephant (*Loxodonta africana* Blumenbach) impacts on vegetation and biodiversity, particularly in southern Africa (Cumming et al., 1997; Skarpe et al., 2004; O'Connor et al., 2007; Guldmond and Van Aarde, 2008; Gandiwa et al., 2011a), as a result of increasing elephant populations in some areas where this species is protected (Valeix et al., 2007; Van Aarde and Jackson, 2007). Similarly, fire occurrence has also been linked to reduced woody vegetation cover in some savanna ecosystems (Bond and Keeley, 2005; Pricope and Binford, 2012).

Anthropogenic and natural disturbances in protected areas may threaten the structure and composition of woody vegetation in savanna areas. Therefore, the study of structure and composition of tropical vegetation becomes more important in the face of the ever increasing threats to the tropical ecosystems (example, Addo-Fordjour et al., 2009). Given that protected areas are the cornerstone of global biodiversity conservation (Gaston et al., 2008); we focused our study on

establishing the status of woody vegetation in a large state protected area occurring in southern Zimbabwe. Specifically, our study objectives were: i) to establish the status of woody vegetation structure and composition and ii) to determine the main factors influencing woody vegetation structure and composition across the Gonarezhou National Park, Zimbabwe.

MATERIALS AND METHODS

Study area

Gonarezhou National Park occurs in southern Zimbabwe between 21° 00' to 22° 15' S and 30° 15' to 32° 30' E (Figure 1), covering ~5000 km². Gonarezhou National Park altitude ranges from 165 to 575 m above sea level. Established in the early 1930s as a Game Reserve, Gonarezhou National Park was upgraded into a national park in 1975 under the Parks and Wildlife Act of 1975. The study area experiences three seasons: hot dry, hot wet and cool dry. Annual average rainfall for Gonarezhou National Park is about 466 mm, with November to March being the wettest months. The dry season normally lasts from April to October. The major vegetation type is *Colophospermum mopane* J. Kirk ex Benth woodland, which covers approximately 40% of Gonarezhou National Park. There is a wide variety of large herbivore species in Gonarezhou National

Table 1. Attributes of woody vegetation variables (mean \pm standard error) for the three strata across Gonarezhou National Park (GNP), Zimbabwe.

Variable	Northern GNP	Central GNP	Southern GNP	Significance (<i>P</i> -value)
Basal area (m ² /ha)	2.33 \pm 9.50 ^a	0.67 \pm 3.33 ^b	0.50 \pm 2.33 ^b	0.003
Woody plant height (m)	4.24 \pm 0.31 ^a	4.36 \pm 0.22 ^a	3.96 \pm 0.21 ^a	0.640
Shrub density/ha	190.89 \pm 21.14 ^a	155.56 \pm 18.12 ^a	235.18 \pm 25.68 ^b	0.018
Stem density/ha	1600.31 \pm 108.35 ^a	1580.99 \pm 85.27 ^a	1748.15 \pm 192.36 ^a	0.723
Tree density/ha	362.89 \pm 40.50 ^a	400.88 \pm 18.29 ^a	364.82 \pm 25.96 ^a	0.081
Browsed plant density/ha	203.23 \pm 42.13 ^a	188.16 \pm 39.34 ^b	176.74 \pm 45.26 ^b	0.009
Fire damaged plant density/ha	56.12 \pm 11.34 ^a	43.21 \pm 13.45 ^a	33.49 \pm 11.53 ^a	0.555
Dead plant density/ha	16.04 \pm 3.30 ^a	14.62 \pm 2.80 ^a	39.51 \pm 18.02 ^a	0.641
Species diversity (<i>H'</i>)	1.25 \pm 0.09 ^a	0.88 \pm 0.07 ^b	0.90 \pm 0.10 ^b	0.003

Significant levels are from one-way ANOVA tests. Different letter superscripts within rows for each variable denote significant differences (Fisher's LSD, $P < 0.05$). Significant values are indicated in bold.

Park, including the African elephant. On average 22% of Gonarezhou National Park is burnt by uncontrolled fire every year and most of these fires are started by illegal hunters inside the park (Gandiwa and Kativu, 2009).

Sampling design and data collection

This study was based on a stratified random sampling design. The study area was divided into three strata based on natural and artificial features (Gandiwa et al., 2012a; Figure 1), namely the northern Gonarezhou National Park (1167 km²) including the area bounded by the Runde and Save rivers (53 sample plots), central Gonarezhou National Park (2963 km²) including the area between Runde River and railway line (57 sample plots) and southern Gonarezhou National Park (820 km²) including the area between the railway line and Mwenezi River (27 sample plots). The number of sample plots per strata was not directly linked to the size of the strata but was chosen to provide reliable information about woody vegetation structure and composition. Sample plots were randomly generated based on the grid intercepts on a topographical map. We used sample plots measuring 20 \times 30 m.

It should be noted that the rivers and railway line used in this study were primarily for physical demarcation of the study strata and are not very effective in containing elephant movements (Gandiwa et al., 2013). However, the rivers and railway line act as good firebreaks for fires in Gonarezhou National Park (*E. Gandiwa*, personal observation). The Save, Runde and Mwenezi rivers are perennial rivers and have high animal concentrations during the dry seasons. The three study strata differ in geology and soils as outlined by Gandiwa et al. (2011b). The elephant densities for the three study strata are 2.18 elephants/km² in northern Gonarezhou National Park; 2.04 elephants/km² in central Gonarezhou National Park and 1.39 elephants/km² in southern Gonarezhou National Park (Dunham et al., 2010).

The woody strata comprised of trees and shrubs. Trees were defined as rooted, woody, self-supporting plants ≥ 3 m in height with one or a few definite trunks whereas shrubs were defined as rooted, woody, self-supporting, multi-stemmed or single stemmed plants greater than 1 m, but < 3 m in height (Gandiwa and Kativu, 2009). Plots were pegged on the ground with four metal pegs and a flexible 100 m measuring tape was laid around the plot perimeter to define the sample plots. For each woody vegetation within the plot, species name, woody plant height, stem circumference, number of stems per plant, fire damage, plant status (alive or dead) and evidence of browse were recorded. Floristic composition and

structure of woody vegetation component were assessed from May to June 2011.

Data analysis

Woody vegetation basal circumference values were converted to basal area whereas all density measures were converted to per ha as outlined by Gandiwa and Kativu (2009). The Shannon-Weiner (*H'*) diversity index (Ludwig and Reynolds, 1988) was used to calculate the woody vegetation diversity values of each sample plot. Data were tested for normality using the Kolmogorov-Smirnov test in STATISTICA Version 6 for Windows software (StatSoft, 2001). Data on mean woody plant height, basal area, density of shrubs, trees, dead plants, fire damaged plants, browsed plants and stems were $\log_{10}(x + 1)$ transformed to satisfy the normality assumption. A

one-way analysis of variance (ANOVA) with strata as categorical predictor and woody vegetation variables as dependent variables was performed to test differences of measured variables across Gonarezhou National Park. For variables with significant differences, Fisher's least significant difference (LSD) *post-hoc* tests were used to determine differences between the three strata. Furthermore, we used an indirect ordination approach, namely the principal component analysis (PCA), to extract the main components of variation in the woody vegetation structure and composition using CANOCO Version 4.5 software for Windows and CanoDraw for Windows (Ter Braak and Šmilauer, 2002).

RESULTS

A total of 4589 individual woody plants, that is trees and shrubs, were assessed in the 137 sample plots and 132 woody plant species were recorded. Trees and shrubs contributed 66 and 34% respectively of the woody plants sampled. Woody vegetation basal area was significantly higher in the northern Gonarezhou National Park than in the central and southern Gonarezhou National Park (Table 1); shrub density was significantly higher in the southern Gonarezhou National Park compared to the central and northern Gonarezhou National Park; browsed plant density was significantly higher in the northern Gonarezhou National Park compared to central and

Table 2. Eigenvalues and variance explained by the Principal Component Analysis.

Axes	1	2	3	4
Eigenvalues	0.30	0.26	0.18	0.14
Cumulative percentage variance of species data	29.60	55.60	73.50	87.10

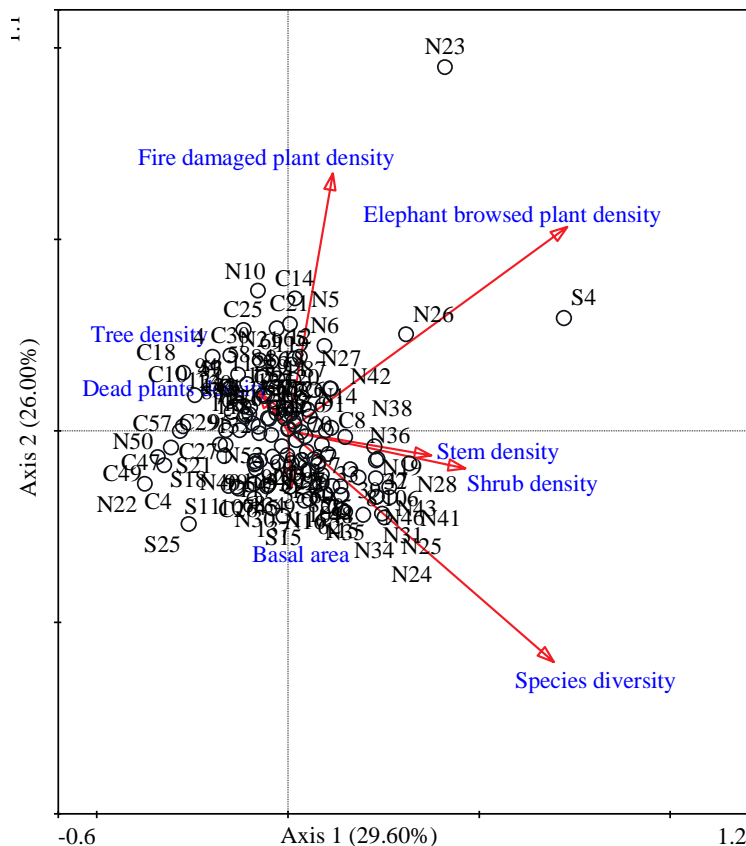


Figure 2. Scatter plot of the sample plots (round circles) in woody vegetation across Gonarezhou National Park, southern Zimbabwe. Notes: N denotes sample plots from northern Gonarezhou National Park; C denotes sample plots from central Gonarezhou National Park, and S denotes sample plots from southern Gonarezhou National Park.

Southern Gonarezhou National Park, and woody species diversity was significantly higher in the northern Gonarezhou National Park compared to the central and southern Gonarezhou National Park (Table 1). The woody vegetation community was dominated by *Acacia nigrescens* Oliv., *Androstachys johnsonii* Prain, *Brachystegia glaucescens* Hutch. and Burt Davy, *C. mopane*, *Combretum apiculatum* Sond., *Dichrostachys cineria* (L.) Wight and Arn., *Diplorhynchus condylocarpon* (Müll. Arg.) Pichon, *Guibourtia conjugata* (Bolle) J. Léonard, *Hyphaene natalensis* Gaertn., *Julbernardia globiflora* (Benth.) Troupin, *Kirkia acuminata* Oliv., *Spirostachys africana* Sond., *Terminalia prunioides* M.A. Lawson, and other riparian and alluvial vegetation species. In contrast, there were no significant differences

in woody plant height, densities of trees, stems, dead plants and fire damaged plants across Gonarezhou National Park.

The PCA output of study vegetation variables shows Axis 1 accounting for 29.60% and Axis 2 accounting for 26.00% of the variance (Table 2). Axis 1 defines a gradient from sample plots with higher tree density and dead plant density to sample plots with higher densities of elephant browsed plants and species diversity. Axis 2 defines a gradient from sample plots with higher species diversity to sample plots with higher densities of fire damaged plants and elephant browsed plants. There was no distinct separation of sample plots in the PCA ordination diagram for the two axes in relation to the study strata across Gonarezhou National Park (Figure 2).



Figure 3. Woody vegetation in Gonarezhou National Park, southern Zimbabwe. Top-left: evidence of woody vegetation damage by elephants, top-right: mopane woodland and bottom: mixed woody vegetation community. Photo credits: P. Zisadza-Gandiwa.

DISCUSSION

The results of the present study show that there were significant differences in basal area, browsed plant density, shrub density and species diversity across the three strata in Gonarezhou National Park. The structural and compositional differences across the three strata in Gonarezhou National Park were possibly related to herbivory, fires, human activities, droughts, geology and soil differences (Tafangenyasha, 1997a, 1998; Gandiwa and Kativu, 2009; Gandiwa et al., 2011a, b). Repeated fires and elephant browsing are known to stress normal growth and affect the health of the woodland and may top-kill woody vegetation (Bond, 2008; Ryan and Williams, 2011; Asner and Levick, 2012). Furthermore, elephant populations in Gonarezhou National Park have over the years continued to increase, from ~3100 in 1969 to ~9100 in 2009 (Dunham et al., 2010). This increase may also have been influenced by the recent non-culling of elephants in the park since the last elephant cull in Gonarezhou National Park was conducted in 1993. Tsetse fly (*Glossina* spp.) (Diptera: Glossinidae) eradication teams cleared riparian woodlands from parts of the major river systems, i.e. Save, Runde and Mwenezi, in Gonarezhou National Park, also negatively influencing the woody vegetation (Gandiwa and Kativu, 2009).

The present study shows that elephant browsing signifi-

cantly affected the woody vegetation structure across Gonarezhou National Park. A higher number of elephant damaged trees were recorded in northern Gonarezhou National Park, particularly on *C. mopane* woodland. This may be a result of mopane being the common species in the study area, hence, increasing the probability of it being targeted by elephants. Larger trees were less damaged by elephants and most damage was recorded on small trees. Field observations showed that elephant damage was characterized by breaking of branches and stems, uprooting, pushing over and scarring of woody species (Figure 3). Trees on hilltops and rocky outcrops were, however, slightly damaged by elephants compared to trees in the plains as also reported by Mpofu et al. (2012). Moreover, a recent study in northern Gonarezhou National Park reported marked woodland degradation on *Acacia tortilis* (Forssk.) Hayne woodland patches as a result of elephant activity (Gandiwa et al., 2011a). Elsewhere, Anderson and Walker (1974) have noted a strong selection for *C. mopane* in Sengwa Wildlife Research Area, Zimbabwe, however, with increased amount of re-growth following high elephant damage.

Elephants often change the structure and composition of vegetation, particularly in areas close to water sources (De Leeuw et al., 2001; Mukwashi et al., 2012). During the wet season, the elephant population is distributed throughout the park, but water supplies, through seasonal water pans, in central Gonarezhou National Park dry up

in the dry season reducing the range of the elephants. Elephants are therefore, forced to move towards permanent water, largely along the Save, Runde and Mwenezi rivers, and artificial water sources such as Masasanya dam and Benji weir, resulting in marked concentration and increased woody vegetation damage in these areas (Tafangenyasha, 1997b; Gandiwa et al., 2012b). Elsewhere, Smit et al. (2007) reported a similar pattern of habitat use by elephants in relation to surface water in Kruger National Park, South Africa. Mosugelo et al. (2002) attributed the conversion of woodland vegetation into shrubland to the strong increase of elephant browsing pressure along the Chobe River, Botswana. Kalwij et al. (2010) reported an increase in tree density, canopy cover and volume in central Chobe, in spite of a growing elephant population. In Maputo Elephant Reserve, Mozambique, Ntumi et al. (2005) reported that elephant habitat occupation was closely linked to forage and water resources.

The present study shows that shrub density was different across Gonarezhou National Park. This may probably be a result of resprouting from the base after being pushed over by elephants and also after being burnt. Our results also show that the majority of trees were multi-stemmed, a situation normally resulting from resprouting in response to disturbances. Disturbance, such as herbivory and repeated fires are likely to promote vigorous resprouting (Bond and Keeley, 2005). We also recorded evidence of large tree mortality, most likely from the interaction of elephant activity, fires, droughts and disease in Gonarezhou National Park, as represented by moderate dead tree densities.

Our results show that woody vegetation structure and composition have some similarities and dissimilarities across Gonarezhou National Park. Variations in woody vegetation structure and composition could be attributed to both natural and anthropogenic disturbance factors. Based on our study findings, we therefore, recommend that management in Gonarezhou National Park should aim at conserving optimal woody vegetation diversity and structure which allows for the effective conservation of wildlife resources in the park. Where possible, extreme woody vegetation degradation, particularly from elephant activity, frequent fires and human activities, should be minimised. Future research should aim to detangle the effects of localised effects of elephants and fires on different woodlands in the park. Moreover, considerations for future large herbivore species re-introductions in Gonarezhou National Park should consider the variations in woody vegetation structure and composition across the park.

ACKNOWLEDGEMENTS

This research was supported by the Gonarezhou Conservation Project, a conservation partnership between the Zimbabwe Parks and Wildlife Management

Authority and Frankfurt Zoological Society. We thank the Director-General and Chief Ecologist of Zimbabwe Parks and Wildlife Management Authority for permission to undertake this study. We are grateful to N.J. Monks, E. Mpofu, S. Chiganze, J. Jakarasi and staff of Gonarezhou National Park for rendering invaluable assistance during fieldwork. We appreciate the constructive comments from three anonymous reviewers which helped improve this manuscript.

REFERENCES

- Addo-Fordjour P, Obeng S, Anning A, Addo M (2009). Floristic composition, structure and natural regeneration in a moist semi-deciduous forest following anthropogenic disturbances and plant invasion. *Int. J. Biodivers. Conserv.* 1(2):021-037.
- Alamu L, Agbeja B (2011). Deforestation and endangered indigenous tree species in South-West Nigeria. *Int. J. Biodivers. Conserv.* 3(7):291-297.
- Anderson GD, Walker BH (1974). Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *J. S. Afr. Wildl. Manage. Assoc.* 4:1-14.
- Asner GP, Levick SR (2012). Landscape-scale effects of herbivores on treefall in African savannas. *Ecol. Lett.* 15:1211-1217.
- Ben-Shahar R (1998). Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecol.* 136(2):189-189.
- Bond WJ (2008). What limits trees in C₄ grasslands and savannas? *Annu. Rev. Ecol. Evol. Syst.* 39:641-659.
- Bond WJ, Keeley JE (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* 20(7):387-394.
- Cumming DHM, Fenton MB, Rautenbach IL, Taylor RD, Cumming GS, Cumming MS, Dunlop JM, Ford AG, Hovorka MD, Johnston DS (1997). Elephants, woodlands and biodiversity in Southern Africa. *S. Afr. J. Sci.* 93(5):231-236.
- De Leeuw J, Waweru MN, Okello OO, Maloba M, Nguru P, Said MY, Hesbon MA, Heitkönig IMA, Reid RS (2001). Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biol. Conserv.* 100:297-306.
- Dunham KM, Van Der WE, Van Der WHF, 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.
- Frost P, Medina E, Menaut JC, Solbrig O, Swift M, Walker B (1986). Responses of Savannas to Stress and Disturbance. *IUBS Special Issue, No. 10*, pp. 1-82.
- Gandiwa E, Chikorowondo G, Zisadza-Gandiwa P, Muvengwi J (2011b). Structure and composition of *Androstachys johnsonii* woodland across various strata in Gonarezhou National Park, southeast Zimbabwe. *Trop. Conserv. Sci.* 4(2):218-229.
- Gandiwa E, Gandiwa P, Mxoxa T (2012a). Structure and composition of *Spirostachys africana* woodland stands in Gonarezhou National Park, southern Zimbabwe. *Int. J. Environ. Sci.* 2(4):2076-2089.
- Gandiwa E, 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), pp Art. #685, 613 pages. DOI: 610.4102/koedoe.v415114101.4685.
- Gandiwa E, Magwati T, Zisadza P, Chinuwo T, Tafangenyasha C (2011a). The impact of African elephants on *Acacia tortilis* woodland in northern Gonarezhou National Park, Zimbabwe. *J. Arid Environ.* 75(9):809-814.
- Gandiwa E, Tupulu N, Zisadza-Gandiwa P, Muvengwi J (2012b). Structure and composition of woody vegetation around permanent-artificial and ephemeral-natural water points in northern Gonarezhou National Park, Zimbabwe. *Trop. Ecol.* 53(2):169-175.

- Gandiwa E, Heitkönig IMA, Gandiwa P, Matsvayi W, Van Der WH, Ngwenya MM (2013). Large herbivore dynamics in northern Gonarezhou National Park, Zimbabwe. *Trop. Ecol.* 54(3):343-352.
- Gaston KJ, Jackson SF, Cantú-Salazar L, Cruz-Piñón G (2008). The ecological performance of protected areas. *Annu. Rev. Ecol. Syst.* 39(1):93-113.
- Guldemond R, Van AR (2008). A meta-analysis of the impact of African elephants on savanna vegetation. *J. Wildl. Manage.* 72(4):892-899.
- Holdo RM (2007). Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecol. Appl.* 17(2):558-568.
- Kalwij JM, De Boer WF, Mucina L, Prins HHT, Skarpe C, Winterbach C (2010). Tree cover and biomass increase in a southern African savanna despite growing elephant population. *Ecol. Appl.* 20(1):222-233.
- Ludwig JA, Reynolds JF (1988). *Statistical ecology. A primer on methods and computing.* John Wiley & Sons, New York.
- Mosugelo DK, Moe SR, Ringrose S, Nellemann C (2002). Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *Afr. J. Ecol.* 40(3):232-240.
- Mpofu E, Gandiwa E, Zisadza-Gandiwa P, Zinhiva H (2012). Abundance, distribution and status of African baobab (*Adansonia digitata* L.) in dry savanna woodlands in Southern Gonarezhou National Park, southeast Zimbabwe. *Trop. Ecol.* 53(1): 119-124.
- Mukwashi K, Gandiwa E, Kativu S (2012). Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange National Park, Zimbabwe. *Int. J. Environ. Sci.* 2(3):1355-1368.
- Ntumi CP, Van Aarde RJ, Fairall N, de Boer WF (2005). Use of space and habitat by elephants (*Loxodonta africana*) in the Maputo Elephant Reserve, Mozambique. *S. Afr. J. Wildl. Res.* 35(2):139-146.
- O'Connor TG, Goodman PS, Clegg B (2007). A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biol. Conserv.* 136(3):329-345.
- O'Kane CAJ, Duffy KJ, Page BR, Macdonald DW (2012). Heavy impact on seedlings by the impala suggests a central role in woodland dynamics. *J. Trop. Ecol.* 28(3):291-297.
- Pricope NG, Binford MW (2012). A spatio-temporal analysis of fire recurrence and extent for semi-arid savanna ecosystems in southern Africa using moderate-resolution satellite imagery. *J. Environ. Manage.* 100:72-85.
- Ryan CM, Williams M (2011). How does fire intensity and frequency affect miombo woodland tree populations and biomass? *Ecol. Appl.* 21(1):48-60.
- Sankaran M, Ratnam J, Hanan N (2008). Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecol. Biogeogr.* 17(2):236-245.
- Scholes RJ, Archer SR (1997). Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28:517-544.
- Skarpe C (1990). Structure of the woody vegetation in disturbed and undisturbed arid savanna, Botswana. *Plant Ecol.* 87(1):11-18.
- Skarpe C, Aarrestad PA, Andreassen HP, Dhillion SS, Dimakatso T, du Toit JT, Halley DJ, Hytteborn H, Makhabu S, Mari M (2004). The return of the giants: ecological effects of an increasing elephant population. *Ambio* 33(6):276-282.
- Smit IPJ, Grant CC, Devereux BJ (2007). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biol. Conserv.* 136:85-99.
- StatSoft (2001). STATISTICA for Windows, version 6, StatSoft Inc. 2300 Tulsa.
- Tafangenyasha C (1997a). Tree loss in the Gonarezhou National Park (Zimbabwe) between 1970 and 1983. *J. Environ. Manage.* 49(3):355-366.
- Tafangenyasha C (1997b). Should Benji Dam be dredged? A preliminary impact assessment to dredging a water reservoir in an African national park. *Environmentalist* 17(3):191-195.
- Tafangenyasha C (1998). Phenology and mortality of common woody plants during and after severe drought in south-eastern Zimbabwe. *Trans. Zimbabwe Sci. Assoc.* 72:1-6.
- Ter Braak CJF, Šmilauer P (2002). *CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5).* Microcomputer Power, Ithaca, New York.
- Valeix M, Fritz H, Dubois S, Kanengoni K, Alleaume S, Said S (2007). Vegetation structure and ungulate abundance over a period of increasing elephant abundance in Hwange National Park, Zimbabwe. *J. Trop. Ecol.* 23(1):87-93.
- Van Aarde RJ, Jackson TP (2007). Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biol. Conserv.* 134(3):289-297.
- Williams R, Duff G, Bowman D, Cook G (1996). Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *J. Biogeogr.* 23(6):747-756.