RESEARCH

Elephants and riparian woodland changes in the Linyanti region, northern Botswana

Gabriella Teren, Norman Owen-Smith*

Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa; email: Teren@gecko.wits.ac.za; Norman.Owen-Smith@wits.ac.za

*Corresponding author

Abstract

The decline of woodlands as a result of elephant disturbance is of much concern for biodiversity conservation in Africa. Northern Botswana supports the largest elephant (*Loxodonta africana*) population and highest local density levels near rivers during the dry season. We describe changes in structure and composition that have occurred in the riparian woodland flanking the Linyanti River, from unpublished reports, theses and our recent observations. There has been a progressive reduction in representation of the two most common *Acacia* spp. as a result of mortality to canopy trees, largely from felling and bark removal by elephants. However, both arboreal species show little regeneration, apart from localized seedlings. Other canopy tree species are less susceptible to damage, but also show a lack of saplings. A dense shrub understorey has developed since 1992, dominated by *Combretum mossambicense*, a species not utilized by elephants although browsed by ruminants. The patchy woodland decline and advancing shrubbery, plus contrasting recruitment patterns of canopy trees versus shrubs, suggest that factors besides elephants—such as climate—might also be involved in woodland change. The study we have initiated will interpret the potential consequences of these changes for woodland biodiversity, building on the spatio-temporal record provided by aerial photography.

Keywords
Botswana, Linyanti, elephant impacts, *Loxodonta africana*; plant biodiversity; riparian vegetation, regeneration

Résumé

Le déclin de la savane boisée par suite aux perturbations de l'éléphant est sujet de beaucoup de soucis en ce qui concerne la conservation de la biodiversité en Afrique. Le Botswana du nord abrite la plus grande population d'éléphants (*Loxodonta africana*) et les plus hauts niveaux de densité locale près des rivières pendant la saison sèche. Nous décrivons les changements dans la structure et la composition qui se sont produits dans la savane boisée riveraine au bord du fleuve Linyanti, d'après les rapports inédits, les thèses et nos observations récentes. L'on a constaté une réduction progressive dans la représentation des deux spp *Acacia* les plus communs suite à la mortalité des arbres à voûte, due en grande partie au terrassement et à l'enlèvement des écorces par les éléphants. Cependant, les deux espèces arboricoles montrent peu de régénération, à part des semis localisés. D'autre espèces d'arbres à voûte sont moins susceptibles au dégât, mais aussi montrent un manque de jeunes arbres. Un sous-étage d'arbrisseaux denses s'est développé depuis 1992, dominé par

Combretum mossambicense, une espèce non utilisée par les éléphants bien que broutée par les ruminants. Le déclin de la savane boisée inégale et les arbrisseaux qui avancent, en plus des configurations contrastées de recrutement d'arbres à voûte contre des arbrisseaux, suggèrent que d'autres facteurs à part les éléphants - tels que le climat - pourraient aussi être impliqués dans le changement de la savane boisée. L'étude que nous avons commencée interprétera les conséquences potentielles de ces changements pour la biodiversité de la savane boisée, en se basant sur les données spatio-temporelles fournies par la photographie aérienne.

Introduction

The consequences of high elephant abundance for vegetation structure and composition, and hence overall biodiversity, are of major concern in conservation (Cumming et al. 1997; Western and Maitumo, 2004; Kerley and Landman 2006; Owen-Smith et al. 2006). The transformation of the riparian woodland adjoining the Chobe River in northern Botswana to a shrub-land punctuated by the trunks of dead trees has been presented as an example of the kind of situation to be avoided elsewhere. However, following a comprehensive assessment, a team comprising both Norwegian and local researchers could not find any adverse consequences of the drastic vegetation changes for animal abundance or diversity, apart from a decline of bushbuck (Addy 1993; Skarpe et al. 2004).

Extremely high elephant concentrations have also developed further upstream along the Linyanti River. Local density estimates during the dry season have increased from 2.8 elephants per km^2 in 1974 (Sommerlatte 1976) to 12 per km^2 in 1987 (Spinage 1990), and while the regional density recently is 4.2 per km (DWNP 2006), it is estimated that local densities in the riparian fringe reach over 20 elephants per km^2 (pers. obs.). However, once the rains arrive these animals disperse widely through northern Botswana and northwards via the Caprivi Strip of Namibia into Angola (Chase and Griffin 2003). The total elephant population currently exceeds 130,000 within an overall range covering 125,000 km^2 (Blanc et al. 2007). A process of woodland conversion is in progress within the Linyanti river-front, offering the opportunity to understand the mechanisms and project the likely end state and consequences for regional biodiversity conservation. Several surveys of the vegetation there have been undertaken, but the results are contained in unpublished reports or theses and thus have not been widely disseminated. We have initiated a detailed investigation of the vegetation changes that have been and are occurring with regard to assessing the implications for plant biodiversity. Hence this article is a summary of what has been documented by past studies and what we observed during our visit to the region at the end of 2006.

Study area

The Kwando River arises in the Angola highlands and flows south-east along the border between northern Botswana and the Caprivi Strip of Namibia to the east of the Okavango River. When it reaches a fault line the river takes a right angle bend and flows east-north-east along the fault line as the Linyanti River, which forms the border between Botswana and Namibia (Fig. 1). This river then enters a swamp region and emerges as the Chobe River. Apart from a narrow area, most of the Linyanti region lies to the west of Chobe National Park, and is managed as a concession (NG 15), previously for hunting and currently for photographic safaris.

Because the terrace follows the fault line south of the river, the riparian woodland on the Botswana side, which is the focus of our study, occupies a fairly narrow region of only a few hundred metres wide. The prevalent tree species include *Acacia nigrescens, A. erioloba*, *Berchemia discolor*, *Diospyros mespiliformis*, *Garcinia livingstonei*, *Ficus* spp., *Combretum imberbe*, with the predominant shrubs being *Croton megalobotrys*, *Combretum mossambicense*, *Philenoptera nelsii* and *Dichrostachys cinerea*. Further south *Colophospermum mopane* woodlands and shrub-lands become predominant on the relatively thin layer of Kalahari sand overlying basalt. Fires have evidently penetrated the riparian zone in the past, from the presence of burnt stumps, but apparently not over the past decade or longer due to the lack of standing grass by the later part of the dry season.

Past studies

The earliest survey of the area by Sommerlatte (1976) during 1973-74 was focused on the 8.5 km region of the Linyanti river-front within Chobe National Park. Overall the density of trees taller than 3 m was 105 per ha, of which *Acacia* spp. constituted 38%. However,

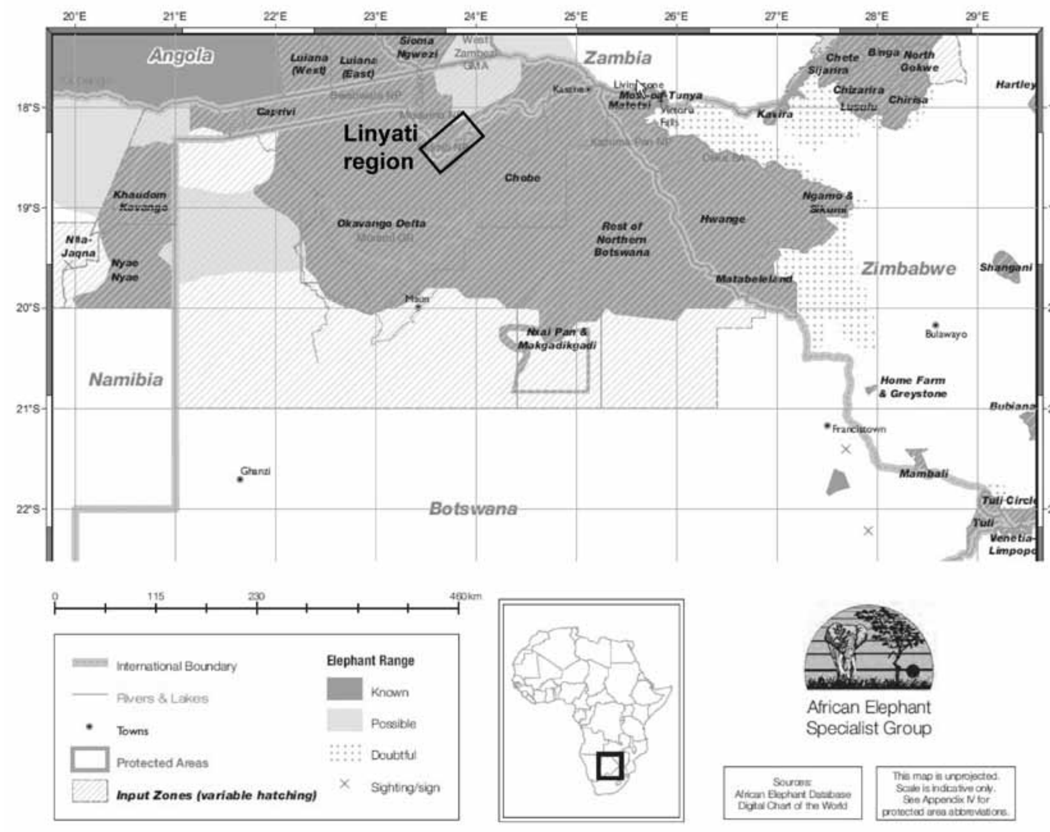

Figure 1. Map of elephant range in northern Botswana showing the Linyanti region (box) on the Botswana– Namibia border. Source: Blanc et al. 2007.

Acacia spp. amounted to only 16.5% of the regeneration layer, with *A. erioloba* poorly represented. From the proportion of dead trees, Sommerlatte estimated an annual loss of 7% of the trees, mostly from the regeneration layer, mainly as a result of uprooting or debarking by elephants. He expressed concern that the recruitment was inadequate to maintain the *Acacia* woodland component. Both *Combretum elaeagnoides* and *Baphia massaiensis* were recorded in the shrub layer.

Wackernagel (1992) conducted a detailed survey of the state of the riparian woodland along transects perpendicular to the river spaced 0.5–1 km apart spanning a 35 km section of the Linyanti riparian woodland. He estimated the total density of trees greater than 20 cm in stem diameter to be around 200 per ha, and summed the density of all woody plants taller than 0.5 m at about 1500 per ha. However, 60% of the *A. erioloba* trees >50 cm in stem diameter and half of the *A. nigrescens* in this size class were dead, while in the 20-50 cm diameter class, fewer than 10% of plants of these two species survived. The representation of *A. erioloba* in the canopy tree layer had declined from 54%, as recorded by Sommerlatte (1976), to 26%. Other tree species showed far lower mortality losses than did these two *Acacia* species. In the shrub or sapling size class, *D. cinerea* showed a mortality loss of around 50%, but very few *A. erioloba* or *A. nigrescens* plants occurred in diameter classes <20 cm. All canopy tree species were poorly represented in the scrub layer <4 cm in stem diameter, with the shrubs *C. mossambicense, D. cinerea* and *C. megalobotrys* predominant. All three of these species were more abundant than was evident at the time of Sommerlatte's survey.

Further, Wackernagel noted that not all tree deaths could be ascribed to elephant damage through felling or bark removal, documenting wind

Figure 2. Remains of a former grove of *Acacia erioloba* trees.

throw as an additional contributing factor. He also found that the strong visually evident patchiness in elephant damage occurred at a smaller scale than the 1 km gap between his transects. Apart from this, only a weak spatial pattern was evident with lower levels of tree damage around the Botswana Defence Force camp and in the region of the Linyanti Explorations Camp. During May 1992 aerial photographic documentation of the state of the riparian woodland was undertaken, obtaining a true-colour mosaic covering the complete 40 km extent of the river front at a scale of 1:10,000.

A further survey by Coulson (1992) in March 1992 encompassed a section of the Kwando River as well, but included only trees (standing or fallen dead as well as alive) greater than 30 cm in stem diameter at breast height. Of 2995 trees recorded, 42.5% were dead. Individual tree species showing high mortality included *Acacia erioloba* (two-thirds dead, most of which appeared recently killed) and *A. nigrescens* (almost 50% dead, mostly recently killed), largely through bark removal. Much lower mortality was recorded for *Philenoptera capassa* (14% dead), *Combretum imberbe* (12% dead) and *C. hereroense* (3% dead). Spatially a higher proportion of trees were dead along the Linyanti River than elsewhere. However, only in a small proportion of cases could tree mortality be ascribed definitely to elephant damage. Elephants were considered to have killed 19% of *A. erioloba* (with 0.7% killed by fire) and 16% of *A. nigrescens* trees, with undetermined or other agents, such as wind, responsible for the remainder. A surprisingly high level of damage apparently caused by wind was noted.

In June 2001 repeat aerial photography was undertaken covering the same area as Wackernagel's (1993) study. Bell (2003) analysed the changes that had taken place in the canopy tree layer (>5 m height), finding an overall net loss of 10.3%, equivalent to an annual rate of 2%. Mortality appeared to be concentrated in the height range 5–13 m, with *A. erioloba* and *A. nigrescens* showing the greatest loss. However, tree felling was patchily concentrated within cells less than 200 m in diameter. The photographs also revealed the widespread prevalence of a dense shrub layer that had not been clearly evident in the 1992 photographs.

Recent observations

During a survey between December 2006 and February 2007 we counted 400 living and dead trees and shrubs in a series of 10–m wide belt transects (unpublished results). From this preliminary investigation and observations throughout the woodland, we noted that only around a third of the large trees of *A. erioloba* and *A. nigrescens* remained alive. The remainder were present as either standing trunks killed by bark removal or felled logs (Fig. 2).

Large specimens of other canopy trees such as *Diospyros mespiliformis* and *Combretum imberbe* showed relatively little damage, because their bark is resistant to removal. Few saplings below 3 m in height were observed, and those present showed much damage through branch or main stem breakage. Some small regenerating plants below 0.5 m in height of *D. mespiliformis* were found, especially on termite mounds, and we observed localized concentrations of small *A. nigrescens* and *C. imberbe* plants. Among sub-canopy trees, almost all *Combretum hereroense* plants had been reducing to coppiced stumps (Fig. 3), compared with 65% of plants showing heavy damage in 1992, with a similar pattern shown by *Peltophorum africanum*. Localized stands of *Terminalia sericea* also existed mostly in the form of resprouting stems. *Croton megalobotrys* showed much less damage and appeared to have increased in abundance.

A dense understorey of *Combretum mossambicense* shrubs had expanded over much of the study area from the east (Fig. 4), while clumps of *Diospyros lycioides* also seemed to be expanding. *Philenoptera nelsii* appeared to have maintained its local prevalence, while *Dichrostachys cinerea* had been reduced mostly to small plants, including seedlings, as well as root sprouts. These shrubs showed an abundance of small size classes from seedlings upwards. The *Colophospermum mopane* trees growing along the margin of the riparian fringe also showed an abundance of all size classes, despite evidence of much damage to stems as well as bark removal and felling by elephants.

Figure 3. Shoot regeneration on *Combretum hereroense* stump.

Discussion

Our recent observations coupled with earlier surveys indicate a progressive reduction of both *Acacia* spp. formerly prevalent in the riparian woodland. Nevertheless, a number of mature trees still remained standing, particularly of *A. nigrescens,* too large to be felled and resistant to further bark removal because of the way their bark has healed over past damage. In contrast, *A. erioloba* seemed less able to regrow bark following its removal by elephants. The standing mature trees continue to produce seeds. However, the lack of any plants in recruitment stages, apart from local patches of *A. nigrescens* seedlings, portends a continuing decline by these tree populations. A similar lack of small specimens of these species was also recorded by Wackernagel (1992), suggesting that this pattern has persisted for 15 years. Since elephants generally only seek out plants taller than 0.5 m (Jachmann and Bell 1985; Mwalyosi 1990), the absence of regeneration suggests the involvement of some other factor, perhaps a persistent desiccation of soil water hindering seedling establishment. It cannot be ascribed to browsing pressure by impala, identified as a major factor along the Chobe River (Skarpe et al. 2004), because impala numbers were low in 1991 and are still only moderate in the Linyanti riparian zone

Figure 4. Dense stand of *Combretum mossambicense* plus *Philenoptera nelsii* shrubbery.

© N. Owen-Smith

Figure 5. Elephant bull feeding amid tall trees of mainly *Diospyros mespilliformis* in the section of the Linyanti riparian woodland near a Defence Force camp.

(2006 regional density: 0.3 impala/km compared with 0.9 impala/km along the Chobe river-front (DWNP 2006)). It seems that most of the decline in the canopy trees between 1992 and 2001 recorded by Bell (2003) was of these two *Acacia* spp. The continuing decline during this period was slow because most trees in the vulnerable size classes had been felled or debarked by elephants prior to 1992. In contrast to the Chobe river-front region, *A. tortilis* is mostly absent from the Linyanti riparian area, and *A. luederitzii* localized in its presence.

Mature *Diospyros mespiliformis* and *Combretum imberbe* are too large to be felled by elephants and have bark that is more resistant to stripping by elephants, and are therefore not directly threatened. A tall shady woodland where these two species predominated remained in the vicinity of the Botswana Defence Force camp, along a dry palaeo-channel (Fig. 5). However, apart from localized patches of small *C. imberbe* seedlings, both species showed very little recruitment. Furthermore, damage by elephants to regenerating stages could curtail plant growth towards canopy height. A similar lack of recruitment by these canopy dominants was documented by Wackernagel (1992). The level of elephant impact on smaller tree species had progressed since 1991 such that almost all specimens of *Combretum hereroense*, *Peltophorum africanum* and *Terminalia sericea* had been reduced to stump coppice. However, these species seemed able to survive in this state, at least for several years.

The dense spread of *Combretum mossambicense* in the shrub layer is reminiscent of an alien plant phalanx, and appears to have developed largely since the 1991 survey by Wackernagel and the time when the 1992 aerial photographs were taken. *C. mossambicense* appears to be unpalatable to elephants, although readily eaten by browsing ruminants (Makhabu 2005). Two other shrubby species have apparently also increased in prominence, although to a more localized extent: *Diospyros lyciodes*, which likewise appears to be little utilized by elephants, and *Croton megalobotrys*, browsed by elephants in the dry season. *Dichrostachys cinerea* has been almost eliminated as a shrub, but persists as root coppice plus abundant seedlings. It had appeared as abundant as *C. mossambicense* in the scrub layer at the time of Wackernagel's survey, while Coulson (1992) also noted dense stands of *D. cinerea* in the area.

It seems evident that a process of woodland conversion is under way, portending the elimination of *Acacia* spp. and gradual decline of other canopy trees due to the paucity of recruitment. This trend suggests the eventual replacement of the woodland by a shrub layer consisting largely of species not eaten by elephants, although palatable to other browsers, paralleling the changes inferred along the Chobe river-front. Elephants are clearly the prime agents of mortality among the larger trees through bark removal, although additional tree felling by wind-throw is often observed following storm events. Elephants are evidently contributing to the suppression of recruitment into the tree layer by retarding the growth of plants in the sapling stage. Carbon fertilization from increased atmospheric CO_2 cannot be ruled out as a factor promoting the invasion by shrub species commonly possessing large underground storage tissues (Bond and Midgely 2000).

However, the extreme lack of canopy species in the seedling or small scrub stage cannot be ascribed to elephants, and other factors seem to be at work. The drying of the swamp on the Caprivi side and apparently reduced flow of the Linyanti River, suggest that a general desiccation in soil moisture may be inhibiting seedling establishment (de Vries et al. 2000; Ringrose et al. 2007). Nevertheless, neither the expanding shrub species nor *C. mopane* shows this limitation. *C. mopane* is recognized as a species adapted to hot, dry conditions in its distribution. There is evidence that tree establishment may take place only at intervals of several decades or even centuries in semi-arid woodlands, while sufficient soil moisture persists long enough to enable seedlings to establish sufficient rooting depth to survive subsequent dry periods (Young and Lindsay 1988).

Our study will focus on establishing spatial variability in the patterns of change shown, particularly with regard to finding localities where tree regeneration may be evident. We will also seek evidence for past vegetation changes from the pollen preserved in former drainage channels or sumps. It has been postulated that the *Acacia* woodland along the Chobe River established during a period towards the end of the 19th century after elephants had been wiped out by human hunting and browser numbers were reduced to low levels by the rinderpest panzootic that spread through Africa around that time (Walker 1986; Skarpe et al. 2004). However, the large *A. erioloba* and *A. nigrescens* trees that were formerly a feature of sections of the Linyanti riparian zone appear to be much older than a century, suggesting that other climatic factors may underlie their establishment. McCarthy et al. (2000) assembled evidence suggesting an 80-year periodicity in water flow in the region. Projecting forwards, the dense shrub layer of species unpalatable to elephants may provide a nursery environment where canopy tree seedlings can eventually establish without being so apparent to elephants (Howe and Miriti 2000; Sharam et al. 2006), but the species benefiting from such conditions are unlikely to be light-demanding *Acacia* spp., although seedlings of species such as *D. mespiliformis* and *G. livingstonei* have been observed under shrubs.

Our study area represents some of the most extreme elephant densities, and hence impacts on vegetation, found anywhere in Africa, but at this stage we cannot make any definite projections about the ultimate consequences for plant diversity in this region. Extrapolating current trends suggests progressive biodiversity loss, but we are aware that ecological processes do not proceed along linear trajectories. Spatial variation in impacts can be to the ultimate benefit of species diversity through benefitting different species in different regions. Much will depend on how the elephants respond to the changing conditions brought about through their impacts, and on how changing climatic conditions influence river flow and soil moisture regimes in the region.

Acknowledgements

Funding for our study was provided by research grants from the National Research Foundation of South Africa and the Wilderness Trust. Research permission was granted by the Ministry of the Environment, Wildlife and Tourism, Botswana. Wilderness Safaris provided logistical support and co-operation.

References

Addy JE. 1993. Impact of Elephant Induced Vegetation Change on the Status of the Bushbuck (*Tragelaphus scriptus ornatus*) along the Chobe River in Northern Botswana. MSc thesis, University of the Witwatersrand, Johannesburg, South Africa.

Bell SM. 2003. Mortality rate of riparian woodland trees of the Linyanti River, northern Botswana. MSc thesis, University of the Witwatersrand, Johannesburg, South Africa.

Ben-Shahar R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* 65:249–256.

Blanc JJ, Barnes RFW, Craig GC, Dublin HT, Thouless CR, Douglas-Hamilton I, Hart JA. 2007. African Elephant Status Report 2007: an update from the African Elephant Database. *Occasional Paper Series of the IUCN Species Survival Commission*, No 33. IUCN/SSC African Elephant Specialist Group, IUCN, Gland, Switzerland. Pp. 122-124.

Bond WJ, Midgley GF. 2000. A proposed CO_2 –controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology*, 6:1–5.

Chase M, Griffin CR. 2003. Ecology, population structure and movements of elephant populations in northern Botswana. *Final Year End Report, Botswana Department of Wildlife and National Parks, Botswana.*

Coulson IM. 1992. Linyanti/Kwando vegetation survey: March 1992. *Report to the Kalahari Conservation Society, Gaborone, Botswana.*

Cumming DHM, Fenton MB, Rautenbach IL, Taylor RD, Cumming GS, Cumming MS, Dunlop JM, Ford GA, Hovorka MD, Johnston DS, Kalcounis M, Mahlangu Z, Portfors CVR. 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* 93:231–236.

de Vries JJ, Selaolo ET, Beekman HE. 2000. Groundwater recharge in the Kalahari, with reference to paleo-hydrologic conditions. *Journal of Hydrology* 238:110–123.

DWNP. 2006. Aerial Census of Animals in northern Botswana Dry Season 2006. *Department of Wildlife and and National Parks, Gabarone, Botswana.*

Howe HF, Miriti MN. 2000. No question: seed dispersal matters. T*rends in Ecology and Evolution* 15:434–436.

Jachmann H, Bell RHV. 1985. Utilization by elephants of the Brachystegia woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology* 23:245–258.

Kerley GIH, Landman M. 2006. The impacts of elephants on biodiversity in the Eastern Cape subtropical thickets. *South African Journal of Science* 102:395–402.

Makhabu SW. 2005. Resource partitioning within a browsing guild in a key habitat, the Chobe riverfront, Botswana. *Journal of Tropical Ecology* 21:641–649.

McCarthy TS, Cooper GRJ, Tyson PD, Ellery WN. 2000. Seasonal flooding in the Okavango Delta, Botswana–recent history and future prospects. *South African Journal of Science* 96:25–33.

Mwalyosi RBB. 1990. The dynamic ecology of Acacia tortilis woodland in Lake Manyara National Park, Tanzania. *African Journal of Ecology* 28:189–199.

Owen-Smith N, Kerley GIH, Page B, Slotow R. van Aarde RJ. 2006. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African Journal of Science* 102:389–394.

Ringrose S, Vanderpost C, Matheson W, Wolski P, Huntsman-Mapila P, Murray-Hudson M, Jellema A. 2007. Indicators of desiccation-driven change in the distal Okavango Delta, Botswana. *Journal of Arid Environments* 68:88–112.

Sharam G, Sinclair ARE, Turkington R. 2006. Establishment of broad-leaved thickets in Serengeti, Tanzania: The influence of fire, browsers, grass competition, and elephants. *Biotropica* 38:599–605

Skarpe C, Aarrestad PA, Andreassen HP, Dhillion SS, Dimakatso T, du Toit JT, Halley DJ, Hytteborn H, Makhabu S, Mari M, Marokane W, Masunga G, Ditshoswane M, More SR, Mojaphoko R, Mosugelo D, Motsumi S, Neo-Mahupeleng G, Ramotadima M, Rutina L, Sechele L, Sejoe TB, Stokke S, Swenson JE, Taolo C, Vandewalle M, Wegge P. 2004. The return of the giants: ecological effects of an increasing elephant population. *Ambio* 33:276–282.

Sommerlatte MWL. 1976. A survey of elephant populations in north-eastern Botswana. *Dept. Wildlife and National Parks; UNDP/FAO; Gabarone Botswana.*

Spinage CA. 1990. Botswana's elephant problem. *Pachyderm* 13:14–19.

Walker B. 1986. In ecology, change brings stability. *Science* 234 (4780):1070–1073.

Wackernagel A. 1993. Elephants and vegetation: severity, scale and patchiness of impacts along the Linyanti River, Chobe district, Botswana. MSc thesis. University of the Witwatersrand, Johannesburg, South Africa.

Western D, Maitumo D. 2004 Woodland loss and restoration in a savanna park: a 20-year experiment. *African Journal of Ecology* 42:111–121.

Young TP, Lindsay WK. 1988. Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands. *African Journal of Ecology* 26:69–72.