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Ecosystems

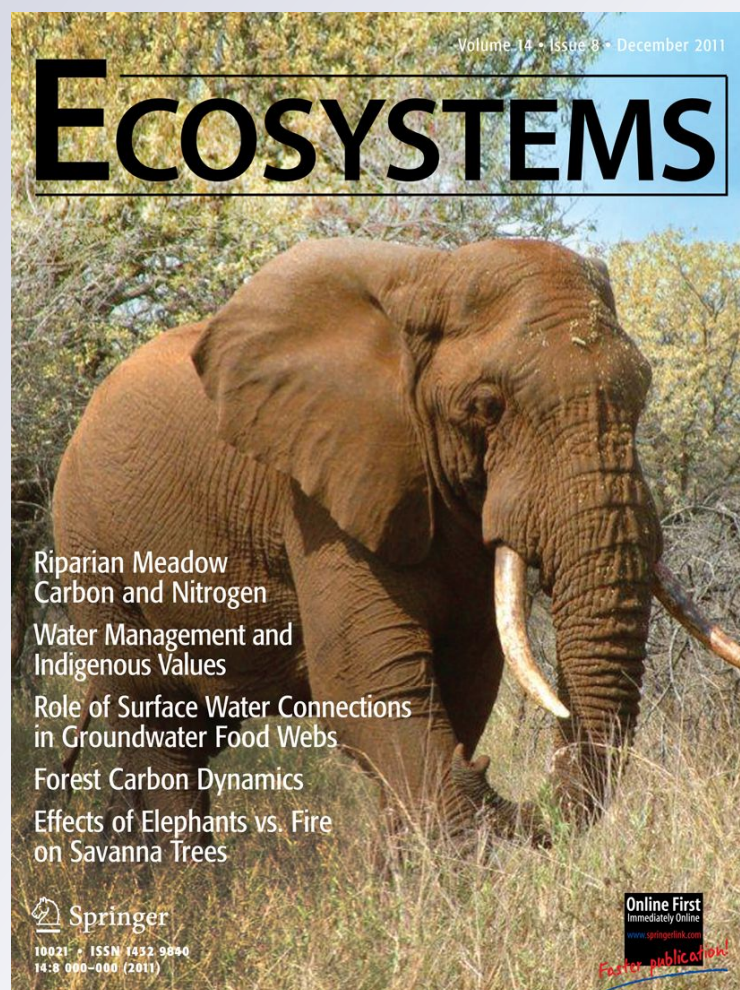
ISSN 1432-9840

Volume 14

Number 8

Ecosystems (2011) 14:1372-1381

DOI 10.1007/s10021-011-9485-z



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Relative Impacts of Elephant and Fire on Large Trees in a Savanna Ecosystem

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ABSTRACT

Elephant and fire are considered to be among the most important agents that can modify the African savanna ecosystem. Although the synergistic relationship between these two key ecological drivers is well documented, it has proved much more difficult to establish the relative effects they have on savanna vegetation structure at a fine-scale over time. In this study, we explore the comparative impacts of fire and elephant on 2,522 individually identified large trees (≥ 5 m in height) in the Kruger National Park, South Africa. Data were collected from 21 transects first surveyed in April 2006 and resurveyed in November 2008, to determine the relative importance of past damage by these agents on subsequent impacts and mortality. The occurrence of fire or elephant damage in 2006 affected the amount of tree volume subsequently removed by both these agents; elephant removed more tree volume from previously burned trees and the impact of subsequent fire was higher on previously burned or elephant-utilized trees than on undam-

aged trees. Mortality was also affected by an interaction between previous and recent damage, as the probability of mortality was highest for trees that suffered from fire or elephant utilization after being pushed over. Subsequent fire damage, but not elephant utilization, on debarked trees also increased the probability of mortality. Mortality was twice (4.6% per annum) that of trees progressing into the ≥ 5 m height class, suggesting an overall decline in large tree density during the 30-month study period. The responses of large trees were species and landscape-specific in terms of sensitivity to elephant and fire impacts, as well as for levels of mortality and progression into the ≥ 5 m height class. These results emphasize the need for fine-scale site-specific knowledge for effective landscape level understanding of savanna dynamics.

Key words: vegetation dynamics; ecological drivers; woody species; savanna management; tree survival; elephant; fire; herbivory.

Received 10 January 2011; accepted 28 August 2011;
published online 27 September 2011

Author Contributions: GS designed the study, performed field data collection, conducted data analysis, and wrote the manuscript; MT and ATV contributed to study design, data analysis, and writing; BRP, RS and RG contributed to study design and writing.

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INTRODUCTION

The co-dominance of trees and grass defines the functioning of the savanna ecosystem, with the relative composition of woody and herbaceous vegetation directly influencing soil quality, hydrology, biomass productivity and rates of transpiration (Breshears and Barnes 1999; Bond 2008). Despite

the established importance of bottom-up drivers such as rainfall and soil, the disturbance effects of fire and herbivory are also considered to play a key role in modifying savanna structure (van Langevelde and others 2003; Levick and others 2009; Staver and others 2009). Of the large herbivores that can directly impact savanna structure, the African elephant (*Loxodonta africana*) is perhaps the most important (Owen-Smith 1992; Kerley and others 2008). The impacts of elephant are mediated by their substantial nutritional demands and foraging behavior—including the pushing over and debarking of large trees—which can result in rapid, direct and profound effects on woody vegetation structure and composition (Shannon and others 2008).

Fire also consumes both woody and grass biomass across savanna ecosystems (Bond and Keeley 2005). However, fire is a non-selective ecological driver, and the extent of impact is largely determined by the size and intensity of the fire (van Wilgen and others 2003; Govender and others 2006), coupled with the susceptibility of individual species (Bond and others 2001). Frequent high intensity fires (*sensu* Govender and others 2006) can reduce woody biomass by killing small recruiting individuals that are unable to escape the fire zone, as well as through top kill of larger well-established trees (van Wilgen and others 2003; Aleper and others 2008). The actions of fire and elephant (and other herbivores) rarely act in isolation from one another, and as a result, complex feedback relationships exist (Dublin and others 1990; Holdo and others 2009; Midgley and others 2010).

Since the late 1960s, there has been concern regarding the decline in large tree densities across a range of African savanna ecosystems, particularly due to the impacts of elephant (Laws 1970). Large savanna trees (≥ 5 m) are of specific interest to ecologists and wildlife managers, as they are considered key structural elements with regard to the functioning of the savanna ecosystem (Manning and others 2006). Large trees provide resources (Jeltsch and others 1996; Dean and others 1999), enhance spatial heterogeneity (Manning and others 2006), and cycle nutrients (Treydte and others 2007). In the Kruger National Park (KNP), South Africa, attention has recently been focused on the possibility that savanna habitats could undergo an irreversible “regime shift” (*sensu* Folke and others 2004) to a less desired state as a result of decline in large tree densities (see Druce and others 2008). Thresholds of potential concern for woody vegetation structure have been developed as a tool for

implementing an adaptive management approach in such situations (Biggs and Rogers 2003). However, empirical data that detail the effects of elephant and fire over time are limited (but see Holdo 2007; Levick and others 2009; Vanak and others in press). Indeed, if a regime shift is likely to occur, then methods to detect this need to be improved (Druce and others 2008).

Although ecological modeling approaches have developed sophisticated predictions of the long-term change in woody cover under different herbivore and fire regimes (Baxter and Getz 2005; Holdo 2007; Holdo and others 2009), they are by their very nature approximations, which focus at comparatively large temporal and spatial scales (Bucini and Hanan 2007). These models therefore provide valuable insights for ecologists exploring broad patterns of savanna function (Sankaran and others 2005). Nonetheless, wildlife managers need to make informed decisions on a site-specific basis, which requires understanding the heterogeneous nature of vegetation dynamics at a more localized scale (Asner and others 2009; Staver and others 2009). This is particularly important because wildlife managers are able to directly manipulate fire and herbivore regimes (Levick and others 2009). One of the most effective approaches to meeting this objective is through the monitoring of individually identified trees (Druce and others 2008). However, the data collected in many previous empirical studies have often focused at inappropriate spatial scales, have not been repeatable, or involved a single-factor approach (Druce and others 2008). Critically, these techniques rarely provide a clear indication as to how the impacts of the main ecological agents drive changes in density, structure, and the relative abundance of species. Investigating these processes can provide crucial understanding of the key factors driving mortality and progression of trees from one height class to the next, particularly how potentially complex interactive effects play out across spatial and temporal scales.

In this study, we demonstrate the effectiveness of a fine-scaled monitoring protocol (Druce and others 2008) in determining the impact of the main ecological drivers (elephant and fire), as well as the effects of disease, on large trees over a 30-month period subsequent to initial description (Shannon and others 2008). We describe the dynamics of large trees, with particular focus on the independent and combined effects of previous elephant utilization and fire impact on subsequent levels of utilization/impact and mortality.

METHODS

Study Area

The data were collected in the southern section of the KNP (25°28–24°91S; 31°95–121.31°32E). The southern section of the KNP is classified into eight broad landscape types: *Acacia* thickets, riverine thickets, lowveld sour bushveld, mountain bushveld, mixed *Combretum/Terminalia* woodland, *Combretum* woodland, *Acacia* marula woodland and thornveld (Gertenbach 1983; Figure 1). There are four perennial rivers that flow west to east in the KNP, including the Sabie and Crocodile Rivers in the southern section of the park (see Shannon and others 2008 for more details). The long-term mean annual rainfall (July–June) at the Skukuza rainfall station was 550 mm (derived from a minimum of 15 years data). During the study period, the annual rainfall in Skukuza was 363 mm in 2006–2007 (35% below average), 470 mm in 2007–2008 (15% below average), and 668 mm in 2008–2009 (20% above average). The drier years of July 2006–July 2008 were characterized by below average monthly rainfall during the latter half of the summer wet season (January–April), and throughout the winter dry season (May–September; see Figure 2).

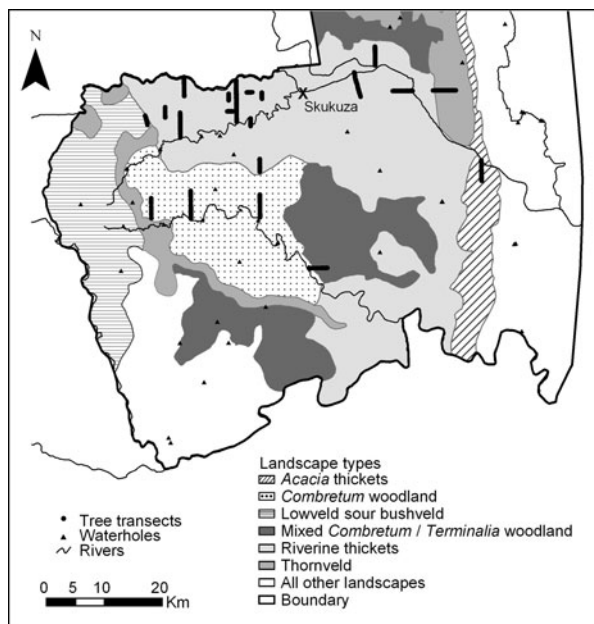


Figure 1. Map of the southern section of Kruger National Park indicating the location of major rivers, water points, landscape types, and the large tree transects.

Data Collection

Surveys of large trees (defined as ≥ 5 m in height, which included mature trees while avoiding shrubs and saplings) were carried out across 22 transects with a combined length of 67 km (Figure 1). The first survey was conducted in April 2006 and the second in November 2008. The inter-survey period encompassed three dry season periods, during which fire intensity and impact on woody vegetation by elephant are typically highest (see Owen-Smith 1992; Shannon and others 2006a; Govender and others 2006). Transects had a strip-width of 10 m and a length that varied between 1.0 and 6.6 km. To ensure that they were straight, a fixed line of latitude or longitude was walked and a GPS was set to track the actual route, and we recorded the location of all trees at least 5 m in height along the transect. Tree height was calculated by placing a 2 m measuring rod next to the tree, while an observer stood at a sufficient distance so that the angle from the ground to the top of the tree was 45° or less. The observer used a ruler to measure the relative height of the tree and the 2 m rod from their perspective. A straightforward division (total tree height in cm/height of measuring rod in cm) provided an accurate measure of true tree height (Zambatis 2005). Each tree was examined for signs of damage by elephant, fire, and disease (for example, wood borer and heart rot of the stem and branches). The extent of utilization by elephant and impacts by fire were estimated as the proportion of the canopy tree volume and/or stem bark circumference that was removed. The data were then classified into one of six broad utilization categories; (1) 1–10%, (2) 11–25%, (3) 26–50%, (4) 51–75%, (5) 76–90%, and (6) 91–100% (see Shannon and others 2008).

The second survey of 21 transects (out of 22 transects) was completed 2.5 years after the first to measure the dynamics of elephant utilization, fire impact, occurrence of disease and mortality over that period. Each of the trees surveyed in 2006 was relocated based on their geographic coordinates and re-assessed for utilization using the criteria described above. The datasheets from 2006 were used to determine the status of each tree at the time of the first survey. Using these data enabled us to evaluate additional utilization/impact that had occurred during the intervening 2.5-year period. We also recorded whether trees suffered mortality. In addition, trees that had entered the ≥ 5 m height class during the 30-month interim period were added to the dataset, along with classification of the species, location, and dimensions (see Shannon and others 2008 for further details).

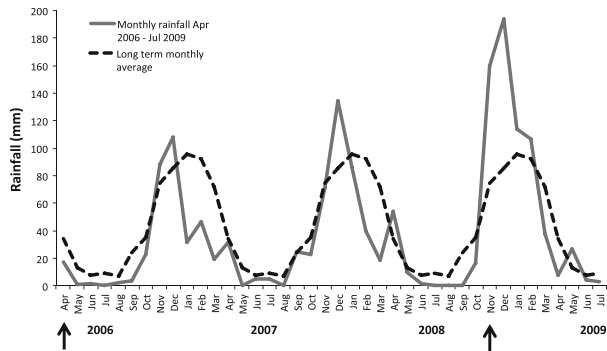


Figure 2. Monthly rainfall (mm) measured at the Skukuza field station from April 2006–July 2009, compared with the long-term monthly average. The *black arrows* indicate the months in which the large tree surveys were carried out.

Data Analysis

Mortality and Progression into the ≥ 5 m Height Class in the Large Tree Guild

We report mortality and the number of trees entering into the ≥ 5 m height class for all species, and separately for the five most abundant species (*Acacia nigrescens*, *Spirostachys africana*, *Sclerocarya birrea*, *Combretum apiculatum* and *Terminalia sericea*). Mortality of trees in four distinct height classes is also detailed, irrespective of species (Table 1, also see Shannon and others 2008).

Impact of Fire, Elephant, and Disease on Trees

We report the proportions of trees that were damaged due to utilization by elephant, impacted by fire or impacted by disease during the 30-month period between the two surveys. For the five most common species and across height classes, we compared the proportions of tree volume removed by elephant and fire using a generalized linear mixed model (GLMM) with species as a random factor and height class and landscape type (Gertenbach 1983) as fixed factors. For all species combined, and then for the five most common species, we examined the relative effects of previous elephant utilization and previous fire impact in determining subsequent tree volume removed by either elephant or fire during the 30-month period between surveys. For both these analyses, we used a GLMM with previous elephant utilization and previous fire damage as random effects, and species and transect as covariates. Proportion of tree volume removed

was arcsine square root transformed for analysis. Where relevant, we report parameter estimates ($\beta \pm SE$) for the comparisons of tree volume removed.

Probability of Mortality as a Function of Elephant, Fire and Disease

Given that elephants contribute to the highest occurrence of damage to trees on this savanna landscape (Shannon and others 2008), we examined the relative importance of the combination of two major types of elephant damage recorded during the 2006 survey (pushed over or debarked) and the subsequent occurrence of elephant utilization, fire or disease in explaining the probability of mortality for these trees (logistic regression with live tree (0) and dead tree (1)). Strength of effects are presented as odds ratios ($e^b \pm SE$).

RESULTS

Mortality and Progression into the ≥ 5 m Height Class in the Large Tree Guild

In 2008, 2,546 individual trees from the total number of trees on the surveyed transects ($n = 2,636$) were relocated (97% success in relocation). Of these, 24 were omitted from the analysis due to missing data. Of the remaining 2,522 trees, 290 trees (11.5%) suffered mortality during the 30-month period between surveys (4.6% per annum; Table 1). Mortality levels of trees in the different height classes ranged from 9.2% for trees in the ≥ 9.6 m height class to 16.3% for trees in the 8.1–9.5 m height class (Table 1). Among the five most common tree species, which constituted 65% of the dataset, mortality levels were highest for *A. nigrescens* (22.4%) and lowest for *S. africana* (1.5%; Table 1). Mortality levels for all other species ranged from 5.6 to 15.7% (Table 1). During the same 30-month period, 136 (5.4%) trees progressed into the ≥ 5 m height class, with *A. nigrescens* (2.6%) and *S. birrea* (0.6%) experiencing the lowest levels, whereas *T. sericea* (16.1%) had the highest number of trees entering into the ≥ 5 m height class (Table 1). Hence, during this period, mortality was 20 times greater than the number of trees that progressed into the large tree height class in *S. birrea*, 8.6 times greater in *A. nigrescens*, and 2.9 times greater in *C. apiculatum*. In contrast, the number of trees entering the ≥ 5 m height class was 3.1 times greater than mortality in *S. africana*, and 2.9 times greater than mortality in *T. sericea*.

Table 1. Numbers and Percentages of Large Trees on 21 Transects in Kruger National Park that were Utilized by Elephant, or Impacted by Fire or Disease during a 30-month Period between 2006 and 2008

	No. of trees surveyed	Utilized by elephant (% of total)	Impacted by fire (% of total)	Impacted by disease (% of total)	Mortality (% of total)	No. of trees entering ≥ 5 m height class (% of total)
All surveyed trees	2,522	581 (20.6)	352 (12.5)	101 (4.0)	290 (11.5)	136 (5.4)
Height class						
Height class 5.0–6.5 m	1,308	292 (22.3)	181 (13.8)	41 (3.1)	134 (10.2)	–
Height class 6.6–8.0 m	742	169 (22.8)	94 (11.3)	34 (4.6)	94 (12.7)	–
Height class 8.1–9.5 m	263	79 (30.0)	36 (13.7)	19 (7.2)	43 (16.3)	–
Height class > 9.6 m	209	29 (14.1)	22 (10.7)	7 (3.3)	19 (9.2)	–
Species						
<i>Acacia nigrescens</i>	577	184 (31.9)	90 (15.6)	33 (5.7)	129 (22.4)	15 (2.6)
<i>Sprostachys africana</i>	539	40 (7.4)	35 (6.5)	9 (1.7)	8 (1.5)	25 (4.6)
<i>Sclerocarya birrea</i>	318	67 (21.1)	45 (14.2)	16 (5.0)	41 (12.9)	2 (0.6)
<i>Combretum apiculatum</i>	299	80 (26.8)	69 (23.1)	4 (1.3)	47 (15.7)	16 (5.4)
<i>Terminalia sericea</i>	123	5 (4.1)	10 (8.1)	2 (1.6)	7 (5.7)	20 (16.3)

The number of trees that suffered mortality and the number that entered into ≥ 5 m height class during the same period are also shown. Numbers are for all surveyed trees, different height classes and the five most common species.

Impact of Fire, Elephant and Disease on Trees

During the 30-month period between surveys, 887 (35%) trees were recorded as being utilized/impacted to some extent, of which a greater number of trees were damaged due to utilization by elephant (20.6%) than by impact from fire (12.5%) or disease (4.0%; Table 1). Among the different height classes, a greater number of trees in the 8.1–9.5 m height class showed elephant utilization (30%) than in any other height class (Table 1). Concomitant with the occurrence of elephant utilization, the proportion of tree volume removed by elephant was higher for trees in the 8.1–9.5 m height class ($\beta = 0.066 \pm 0.022$ SE) and lower for trees in the >9.5 m height class ($\beta = -0.140 \pm 0.030$ SE) compared to trees in the 5–6.5 m height class. The proportion of tree volume removed by fire was similar across height classes, but a greater number of trees in the 8.1–9.5 m height class showed signs of disease (Table 1).

On a species basis, a greater number of *A. nigrescens* (31.9% of individuals) and *C. apiculatum* (26.8%) were utilized by elephant than any of the other common species (Table 1). Fire impact was also most prevalent for *C. apiculatum* (23.1% of individuals) than for any of the other species. In addition to the high occurrences of elephant and fire damage, the proportion of tree volume removed by both these agents was highest in *C. apiculatum* (elephant: $\beta = 0.151 \pm 0.037$ SE; fire: $\beta = 0.105 \pm 0.037$ SE). Elephant, but not fire, was the main agent of tree volume removed for *A. nigrescens* ($\beta = 0.200 \pm 0.039$ SE) and *S. birrea* ($\beta = 0.082 \pm 0.038$ SE). Tree volume removed by both these agents was lowest for *S. africana* and *T. sericea*. Overall, occurrences of disease were low (1.3–5.7% of individuals) for the five common species (Table 1).

Among the landscape types, trees in the lowveld sour bushveld showed the highest proportion of tree volume removed by elephant ($\beta = 0.429 \pm 0.057$ SE), with lower levels on the other five landscape types. Fire-induced removal of tree volume was also highest in the lowveld sour bushveld ($\beta = 0.417 \pm 0.058$ SE), with lower levels in the *Combretum* woodland ($\beta = 0.082 \pm 0.037$ SE) and riverine thickets ($\beta = 0.139 \pm 0.033$ SE), compared to the thornveld landscape. We found no occurrence of fire damage to large trees on the *Acacia* thickets and on the mixed *Combretum*/*Terminalia* woodland landscapes.

During the inter-survey period, 7% of the resurveyed trees were in areas that burned twice,

44% in areas that burned once, whereas 49% of the trees remained in areas that were unaffected by fire. For all tree species, the proportion of tree volume removed by fire during the 30-month period between surveys was significantly affected by whether the tree suffered previous elephant utilization or previous fire impact (fire–elephant interaction: $F_{1,2518} = 6.919$, $P = 0.009$, Figure 3A). Specifically, the effect of elephant utilization in 2006 was similar to the effect of fire impact in 2006 in that the proportion of subsequent tree volume removed by fire was similar when either of these agents acted alone (Figure 3A). When neither fire impact nor elephant utilization was seen in 2006, subsequent tree volume removed by fire was lower (Figure 3A). The combination of previous elephant utilization and previous fire impact were not additive in their effects on subsequent tree volume removed by fire (Figure 3A). For all trees surveyed, species ($P < 0.001$) was a strong covariate of tree volume removed by fire, and *post hoc* analyses of the five most common species showed that the effect of previous fire impact and previous elephant utilization depended on the species. Tree volume removed by fire in *A. nigrescens* increased by 1.11 times if a tree was previously utilized by elephant ($\beta = 0.108 \pm 0.035$ SE). The volume of tree removed by fire was highest for *S. africana* ($\beta = 0.117 \pm 0.050$ SE) and *C. apiculatum* ($\beta = 0.265 \pm 0.108$ SE) if these trees suffered from previous fire damage and were also previously utilized by elephant. There was little effect of previous damage on subsequent tree volume removed by fire for *S. birrea* and *T. sericea*. Transect was a strong covariate when explaining tree volume removed by fire for only *A. nigrescens* ($\beta = 0.012 \pm 0.003$ SE), indicating that certain areas with this species were more prone to burning.

When elephant was the agent of damage, we also found an interaction between previous elephant utilization and previous fire damage on the proportion of tree volume subsequently removed ($F_{1,2518} = 4.015$, $P = 0.045$, Figure 3B). Tree volume removed by elephant in 2008 was highest for trees that were previously burned but not previously utilized by elephant (Figure 3B). Similar to the effects on subsequent fire, the combination of previous elephant utilization and previous fire impact were not additive in their effects on subsequent tree volume removed by elephant (Figure 3B). As seen with fire effects, species ($P < 0.001$) was a strong covariate of tree volume removed by elephant, and *post-hoc* analyses of the five most common species showed that the effect of previous fire impact and previous elephant utili-

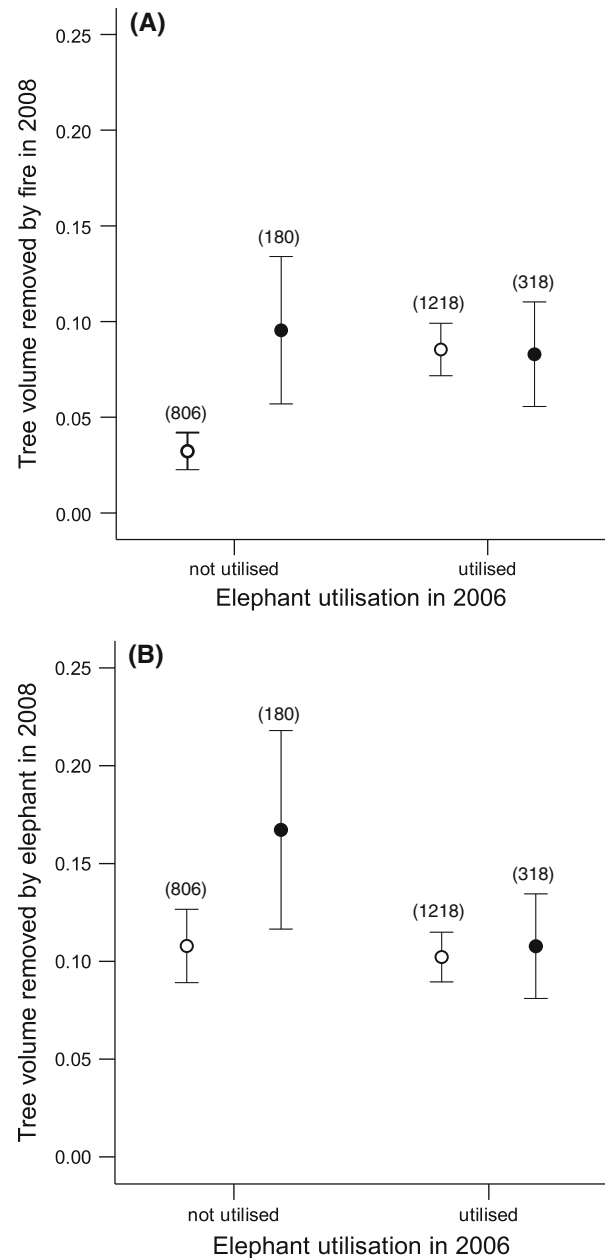


Figure 3. Proportion of tree volume removed (mean \pm 95% CI) by **A** fire impact or **B** elephant utilization during the 30-month interval between surveys. Trees were categorized by whether they had exhibited elephant utilization or fire impact (*open points* = no fire, *closed points* = fire) during the initial survey in 2006. Sample sizes of individual trees are reported above each point.

zation depended on the species. For *S. birrea* ($N = 318$), tree volume removed by elephant increased by 1.16 times if a tree was previously burned ($\beta = 0.148 \pm 0.074$ SE). Similarly, for *A. nigrescens* ($N = 577$), tree volume removed by elephant increased by 1.23 times if a tree was previously burned ($\beta = 0.189 \pm 0.082$ SE) but de-

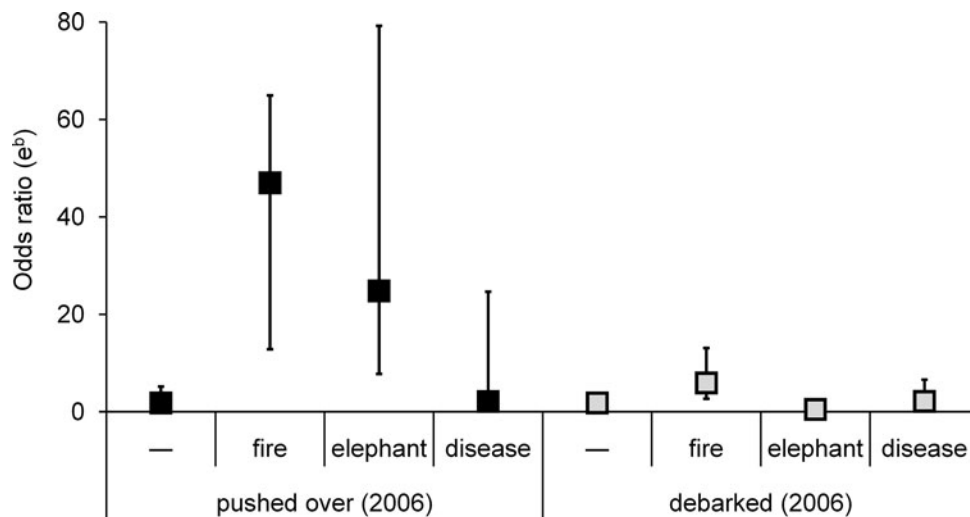


Figure 4. Probability of mortality (odds ratio $e^b \pm 95\%$ CI) for trees that were recorded as pushed over or debarked in 2006 and subsequently impacted by fire, elephant, or disease in the following 30 months.

creased by 1.11 times if it was previously utilized by elephant ($\beta = -0.106 \pm 0.041$ SE). For *C. apiculatum*, subsequent tree volume removed by elephant also decreased by 1.18 times if the tree was previously utilized by elephant ($\beta = -0.167 \pm 0.054$ SE). There was little effect of previous damage on subsequent tree volume removed by elephant for *S. africana*, and *T. sericea*. Transect was a strong covariate when explaining tree volume removed by elephant for *S. africana* ($\beta = 0.004 \pm 0.001$ SE) and *C. apiculatum* ($\beta = 0.016 \pm 0.004$ SE) indicating that elephant damage on trees of these species was spatially clustered.

Probability of Mortality as a Function of Elephant, Fire and Disease

Trees that were recorded as pushed over or debarked in 2006 were twice as likely to die by 2008 compared to trees that did not suffer any damage in 2006 (Figure 4). However, probability of mortality was higher for trees that suffered repeated damage, but the specific combinations of elephant, fire and disease differed in their relative contribution to mortality (Figure 4). Specifically, for trees that were pushed over in 2006, probability of mortality was 47 times higher if they suffered from subsequent fire and 25 times higher if they were further utilized by elephant (Figure 4). Debarked trees with subsequent fire damage were six times more likely to die but subsequent elephant utilization had no additional effect on the probability of mortality (Figure 4). Subsequent disease on trees that were pushed over or debarked also had no

additional effect on the probability of mortality (Figure 4).

DISCUSSION

Focussing on trees in the ≥ 5 m height class provided us with a valuable opportunity to track utilization, impact, and mortality of over 2,500 individual mature trees (comprising 42 species) across the landscape of the southern section of KNP. The discrete spatial distribution and conspicuous nature of large trees enabled us to achieve a high level of success in relocating individuals, confirming the application of this method as a longer term monitoring approach (Druce and others 2008). Our results highlight that there is a high level of utilization and impact on large trees in the southern section of KNP, with approximately a third of the trees surveyed exhibiting a change in state over the 30-month study period.

A greater number of trees were utilized by elephant than were impacted by fire or disease, presenting further evidence of the key role that elephant play in modifying savanna structure over time (Mosugelo and others 2002; Holdo 2007; Shannon and others 2008), whereas fire is a key secondary, and interacting factor. Despite evidence that elephant exhibit a preference for certain habitats (Shannon and others 2006b) and woody species (Shannon and others 2008), our data suggest that they do not target trees that have previously been utilized to a greater extent than ones that had not. In fact, elephant removed more tree volume from trees that were previously burned, a novel

finding, which may indicate that fire events are in fact facilitating the foraging behavior of elephants at the plant-scale, potentially allowing them to take advantage of post-fire flush. Intense utilization by elephant was also the main driver of mortality, as the probability of an individual dying was dramatically higher for trees that suffered subsequent damage (by fire or elephant) after being pushed over or debarked by elephant. It is important to note that during the study period annual rainfall was below the long-term mean, and although not severe enough to be considered a drought, grass production was likely to be significantly affected, particularly as monthly rainfall was distinctly lower than average in the late wet season (Dye and Spear 1982). During such dry periods, elephant are predicted to switch their diet from grass to woody species earlier and browse more intensively (O'Connor and others 2007), which ultimately could lead to greater impacts on large trees.

Although it has commonly been suggested that fire plays only a minor role in the mortality of large trees (Bond and others 2001; Higgins and others 2007), our study demonstrates that the effects of fire events, especially in combination with elephant utilization, can reduce vigor and ultimately lead to the death of a tree. Furthermore, despite being considered above the 'fire trap' (Higgins and others 2007), large trees remain susceptible to mortality as a result of fires damaging the stem and canopy (Moncrieff and others 2008; Midgley and others 2010). The effects of fire were most evident when operating in combination with elephant utilization (Dublin and others 1990; Holdo and others 2009). Indeed, the past actions of elephant foraging (for example, bark stripping, tree-pushing, and branch removal) and fire impact increase the susceptibility of the tree to fire damage in the future (Moncrieff and others 2008) to such an extent, that fire was the leading cause of mortality for trees that had been recorded as pushed-over or debarked by elephant, yet remained alive in 2006. These trees have effectively been placed back in the fire-trap, either as a result of their canopy being toppled or the bark being removed at a susceptible point on the trunk of the tree. Moreover, trees that are pushed over provide increased fuel loads for subsequent fire events. Our results illustrate that impacts from fire, as well as elephant, may only become apparent over time (Aleper and others 2008), further highlighting the need for a repeat monitoring approach, particularly as the long-term effects can be both severe and species-specific.

Of the five most common species in the large tree guild of southern KNP, *A. nigrescens*, *C. apiculatum*

and *S. birrea* all experienced relatively high levels of tree volume removed by elephant and fire; however the impacts on *S. birrea* were lower than for the other two species. An interesting finding in light of the fact that *S. birrea* is considered a highly preferred tree species for elephant (Jacobs and Biggs 2002; Shannon and others 2008; Helm and others 2009). In fact, the status of *S. birrea* in KNP has been cause for specific concern (see Helm and others 2009), but as our data suggest, the very low level of progression for this species into the larger height classes may also be a significant driving force in the decline of mature adult trees, a finding that concurs with results from Helm and others (2009). With regard to differences between trees based on height, individuals in the 8.1–9.5 m height class exhibited the highest levels of elephant utilization.

During the 30-month study period, mortality levels of large trees (all species) were comparable (4.6% per annum) to those from other studies of southern African savannas (for example, 5%, Shackleton 1997; 4%, Trapnell 1959). However mortality during our study period was twice that of progression into the ≥ 5 m height class, but this pattern was species-specific. Mortality rates exceeded rates of progression into the ≥ 5 m height class in some palatable species, such as *A. nigrescens*, *C. apiculatum*, and *S. birrea*, whereas in less palatable species such as *S. africana* and *T. sericea*, the number of trees that entered the large tree height class was greater than the number that died. This suggests that, at current rates of mortality and progression, the composition and structure of the large tree guild may well change across the study area with a decline in some palatable species, whereas less favored and more fire resistant species may increase in density. These changes are also spatially and temporally heterogeneous, being dependent upon the intensity of elephant utilization and fire impact in different landscapes and habitats (Eckhardt and others 2000; Vanak and others, in press). Indeed, the results presented here indicate that there were significant differences in the levels of impact among landscape types, with the lowveld sour bushveld experiencing the highest levels of tree volume removal by both fire and elephant during the study period, concurring with spatial patterns of large tree mortality (see Vanak and others, in press). However, it is important to note that a dataset, which spans 2.5 years, is unable to capture the medium to long-term cycles that are characteristic of savanna dynamics (Scholes and Archer 1997; Sinclair and others 2007), especially because the reasons for apparent low rates of trees progressing into the large height class

between the surveys are beyond the scope of this study. Nonetheless, key factors are likely to include herbivory and fire which prevent growth into larger height classes (Staver and others 2009), the effects of environmental variation in determining the establishment of new cohorts (for example, rainfall: Walker and others 1986) and the impact and periodicity of episodic events (Prins and van der Jeugd 1993; Kraaij and Ward 2006; Chafota and Owen-Smith 2009). In addition, given the comparatively low levels of rainfall during the second half of the wet season in 2007 and 2008 (Figure 2), the growth response of savanna trees may have declined, resulting in fewer trees entering into the large height class.

In conclusion, our results highlight the synergistic relationship between fire, elephant, and abiotic factors in driving the utilization and mortality of large trees in this savanna system. These impacts, operating in conjunction with increasing elephant population densities (Kerley and others 2008), may be sufficient to cause this ecosystem to undergo a regime shift (*sensu* Folke and others 2004). It is therefore essential that monitoring be focused at measuring appropriate leading indicators of change over time (Carpenter and others 2008). Ecosystem management should take an integrated adaptive approach that considers the synergistic relationships between the different ecological drivers rather than looking at their effects in isolation. Our results emphasize the differences in responses at a species-specific level as well as the broader population demographics. Future directions for research need to focus on understanding the spatial variation in these dynamics and the heterogeneity in persistence over time, before a truly reflective threshold of potential concern (Biggs and Rogers 2003) can be set for large tree persistence in African savannas.

ACKNOWLEDGMENTS

We are grateful to SANParks for providing access to the study site, while SANParks game scouts are thanked for providing valuable knowledge and ensuring the safety of the research team during the fieldwork. We thank H. Eckhardt for help in designing the 2006 survey, and D. Druce and A. Smith for assistance in collecting the data. This study was funded by Distell (Pty) Ltd through a donation to the Amarula Elephant Research Programme, University of KwaZulu-Natal (UKZN), and the National Research Foundation (Grant to RS: FA2006032300024). UKZN provided Post-Doctoral Fellowships to GS, MT and ATV.

REFERENCES

- Aleper D, Lye KA, Moe SR. 2008. Response of *Acacia sieberiana* to repeated experimental burning. *Rangel Ecol Manage* 61:182–7.
- Asner GP, Levick SR, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS, Martin RE. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *Proc Natl Acad Sci USA* 106:4947–52.
- Baxter P, Getz W. 2005. A model-framed evaluation of elephant effects on tree and fire dynamics in African savannas. *Ecol Appl* 15:1331–41.
- Biggs HC, Rogers KH. 2003. An adaptive system to link science, monitoring, and management in practice. In: Du Toit JT, Rogers KH, Biggs HC, Eds. *The Kruger experience: ecology and management of savanna heterogeneity*. Washington (DC): Island Press. p 59–80.
- Bond W. 2008. What limits trees in C4 grasslands and savannas? *Ann Rev Ecol Evol Syst* 39:641–59.
- Bond WJ, Keeley JE. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol Evol* 20:387–94.
- Bond WJ, Smythe K, Balfour DA. 2001. *Acacia* species turnover in space and time in an African savanna. *J Biogeogr* 28:117–28.
- Breshears DD, Barnes FJ. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. *Landscape Ecol* 14:465–78.
- Bucini G, Hanan NP. 2007. A continental-scale analysis of tree cover in African savannas. *Glob Ecol Biogeogr* 16:593–605.
- Carpenter SR, Brock WA, Cole JJ, Kitchell JF, Pace ML. 2008. Leading indicators of trophic cascades. *Ecol Lett* 11:128–38.
- Chafota J, Owen-Smith N. 2009. Episodic severe damage to canopy trees by elephants: interactions with fire, frost and rain. *J Trop Ecol* 25:341–5.
- Dean W, Milton S, Jeltsch F. 1999. Large trees, fertile islands, and birds in arid savannas. *J Arid Environ* 41:61–78.
- Druce D, Shannon G, Page BR, Grant R, Slotow R. 2008. Ecological thresholds in the savanna landscape: developing a protocol for monitoring the change in composition and utilization of large trees. *PLoS ONE* 3:e3979.
- Dublin HT, Sinclair ARE, Mcglade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti Mara Woodlands. *J Anim Ecol* 59:1147–64.
- Dye PJ, Spear PT. 1982. The effect of bush clearing and rainfall variability on grass yield and composition in south-west Zimbabwe. *Zimb J Agric Res* 20:103–17.
- Eckhardt HC, van Wilgen BW, Biggs HC. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa between 1940 and 1998. *Afr J Ecol* 38:108–15.
- Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Ecol Evol Syst* 35:557–851.
- Gertenbach W. 1983. Landscapes of the Kruger National Park. *Koedoe* 26:60–82.
- Govender N, Trollope WSW, Van Wilgen BW. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *J Appl Ecol* 43:748–58.

- Helm CV, Witkowski ETF, Kruger L, Hofmeyr M, Owen-Smith N. 2009. Mortality utilization of *Sclerocrya birrea* subsp. *Caffra* between 2001 and 2008 in the Kruger National Park, South Africa. *S Afr J Bot* 75:475–84.
- Higgins SI, Bond WJ, February EC, Bronn A, Euston-Brown DIW, Enslin B, Govender N, Rademan L, O'Regan S, Potgieter LF, Scheiter S, Sowry R, Trollope L, Trollope WSW. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* 88:1119–25.
- Holdo R. 2007. Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecol Appl* 17:558–68.
- Holdo RM, Holt RD, Fryxell JM. 2009. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecol Appl* 19:95–109.
- Jacobs OS, Biggs R. 2002. The status and population structure of the marula in the Kruger National Park. *S Afr J Wildl Res* 32:1–12.
- Jeltsch F, Milton S, Dean W, van Rooyen N. 1996. Tree spacing and coexistence in semiarid savannas. *J Ecol* 84:583–95.
- Kerley GIH, Landman M, Kruger L, Owen-Smith N, Balfour D, de Boer WF, Gaylard A, Lindsay K, Slotow R, Scholes RJ. 2008. Effects of elephants on ecosystems and biodiversity. In: Scholes RJ, Mennell KG, Eds. *Elephant management: a scientific assessment for South Africa*. Johannesburg: Wits University Press. p 101–44.
- Kraaij T, Ward D. 2006. Effects of rain, nitrogen fire and grazing on tree recruitment and survival in bush-encroached savanna, South Africa. *Plant Ecol* 186:235–46.
- Laws RM. 1970. Elephants as agents of habitats and landscape change in East Africa. *Oikos* 21:1–15.
- Levick SR, Asner GP, Kennedy-Bowdoin T, Knapp DE. 2009. The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biol Conserv* 142:1693–700.
- Manning AD, Fischer J, Lindenmayer DB. 2006. Scattered trees are keystone structures—implications for conservation. *Biol Conserv* 132:311–21.
- Midgley JJ, Lawes MJ, Chamaillé-Jammes S. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Aust J Bot* 58:1–11.
- Moncrieff G, Kruger LM, Midgley JJ. 2008. Stem mortality of *Acacia nigrescens* induced by the synergistic effects of elephants and fire in Kruger National Park, South Africa. *J Trop Ecol* 24:655–62.
- 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* 40:232–40.
- 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* 136:329–45.
- Owen-Smith RN. 1992. *Megaherbivores: the influence of very large body size on ecology*. Cambridge: Cambridge University Press.
- Prins HHT, van der Jeugd HP. 1993. Herbivore population crashes and woodland structure in East Africa. *J Ecol* 81:305–14.
- Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N. 2005. Determinants of woody cover in African Savannas. *Nature* 438:846–9.
- Scholes R, Archer S. 1997. Tree-grass interactions in savannas. *Annu Rev Ecol Syst* 28:517–44.
- Shackleton CM. 1997. The prediction of woody productivity in the savanna biome, South Africa. PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.
- Shannon G, Page BR, Duffy KJ, Slotow R. 2006a. The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia* 150:344–54.
- Shannon G, Page B, Slotow R, Duffy K. 2006b. African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *Afr Zool* 41:37–44.
- Shannon G, Druce DJ, Page BR, Eckhardt HC, Grant R, Slotow R. 2008. The utilization of large savanna trees by elephant in southern Kruger 475 National Park. *J Trop Ecol* 24:281–9.
- Sinclair ARE, Mduma SAR, Hopcraft JGC, Fryxell JM, Hilborn R, Thirgood S. 2007. Long-term ecosystem dynamics in the Serengeti: lessons for conservation. *Conserv Biol* 21:580–90.
- Staver AC, Bond WJ, Stock WD, van Rensburg SJ, Waldram MS. 2009. Browsing and fire interact to suppress tree density in an African savanna. *Ecol Appl* 19:1909–19.
- Trapnell CG. 1959. Ecological results of woodland burning in Northern Rhodesia. *J Ecol* 47:161–72.
- Treydte AC, Heitkonig IMA, Prins HT, Ludwig F. 2007. Trees improve grass quality for herbivores in African savannas. *Perspect Plant Ecol Evol Syst* 8:197–205.
- van Langevelde F, van De Vijver C, Kumar L, van De Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Strosnijder L, Bond WJ. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–50.
- Van Wilgen BW, Trollope WSW, Biggs HC, Potgieter ALF, Brockett BH. 2003. Fire as a driver of ecosystem variability. In: Toit JT, Rogers KH, Biggs HC, Eds. *The Kruger experience: ecology and management of savanna heterogeneity*. Washington (DC): Island Press. p 149–70.
- Vanak AT, Shannon G, Thaker M, Page B, Grant R, Slotow R. Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in an African savanna. *Ecography* (in press). doi:10.1111/j.1600-0587.2011.07213.x.
- Walker BH, Stone L, Henderson L, Venede M. 1986. Size structure analysis of the dominant trees in a South African Savanna. *J S Afr Bot* 52:397–402.
- Zambatis N. 2005. Field procedures for veld condition assessment in the Kruger National Park (second revision). Unpublished internal report, SANParks, Skukuza.