Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998

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Abstract

Changes in the cover and density of shrubs and trees were assessed from aerial photographs (1940, 1974 and 1998) as well as from fixed-point photographs taken in 1984 and 1996 in the Kruger National Park, South Africa. Woody cover (trees and shrubs combined) increased by 12% on granite substrates but decreased by 64% on basalt substrates over the past 58 years. Both these figures are expressed in terms of the initial values, respectively. The density of the large tree component of woody vegetation decreased on both substrates. Woody vegetation cover declined as fire return periods became shorter, but the relationship was weak. The increases in woody plant density and cover on granite are thought to be the result of decreased competition from grasses, which in turn is a result of overgrazing by wild herbivores whose numbers have been kept high through the provision of surface water. These effects were not seen on the relatively nutrient-rich basalts, where grasses can recover rapidly even after heavy grazing. The decline in overall woody cover on basalts is interpreted as a result of regular, short-interval prescribed burning over the past 40 years, while the universal decline in large trees seems to result from an interaction between regular, frequent fires and utilization by elephants. The implications for management are discussed.

Key words: aerial photographs, elephants, fire, woody vegetation

Résumé

On a évalué les changements du couvert et de la densité des arbustes et des arbres à partir de photos aériennes (1940, 1974 et 1998) et de photos prises d'un endroit fixe en 1984 et en 1996 dans le Parc National Kruger, en Afrique du Sud. Le couvert boisé (arbustes et arbres pris ensemble) a augmenté de 12% sur les substrats granitiques mais diminué de 64% sur les substrats basaltiques, au cours des 58 dernières années. Ces deux chiffres sont exprimés en termes de valeurs initiales, respectivement. La densité de la composante de grands arbres de la végétation boisée a diminué sur les deux substrats. Le couvert végétal boisé a diminué alors que les périodes de récupération entre les feux raccourcissaient, mais la relation est faible. On pense que l'augmentation de la densité et du couvert boisés sur le granite est le résultat d'une diminution de la compétition exercée par les herbes qui elle, résulte d'un surpâturage des herbivores sauvages dont le nombre a été maintenu élevé par l'apport d'eau de surface. On n'a pas observé ces effets sur les basaltes relativement riches en nutriments, car les herbes peuvent y repousser rapidement même après un pâturage intense. On interprète le déclin du couvert boisé global sur le basalte comme le résultat des feux provoqués régulièrement et avec de brefs intervalles depuis 40 ans, alors que le déclin général des grands arbres semble être le résultat d'une interaction entre les feux, réguliers et fréquents, et la présence des éléphants. On discute de ce que cela implique pour la gestion.

Introduction

South Africa's Kruger National Park is one of the largest conservation areas in Africa. It was proclaimed as a national park in 1926, and covers almost 2 million ha. Since then, it has been closely monitored and managed, making it one of the largest and most intensely managed savanna areas in Africa. Although management aims

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have changed over time, for much of the park's history, they have been aimed in one way or another at the conservation of large mammals. The management has consisted of the following activities:

(i) Culling, initially of carnivores to allow game populations to build up, and later also of herbivores for a variety of reasons; however, no culling is currently practised.

(ii) The provision of surface water by damming seasonal rivers and sinking boreholes, so as to enable large mammals to utilize grazing away from perennial water sources on a continuous rather than a seasonal basis.

(iii) Fencing the boundaries of the park to prevent migration of large mammals beyond the park borders.

(iv) Introducing a programme of prescribed burning, in which vegetation was burnt on a 3-year cycle.

(v) The building of roads and firebreaks for game viewing, access for maintenance of boreholes, for patrolling, and for conducting the prescribed burning programme.

The management options that tend to be most keenly debated are those addressing the manipulation of elephant populations (Pienaar, van Wyk & Fairall, 1966; van Wyk & Fairall, 1969; Coetzee *et al.*, 1979; Hall-Martin, 1990; Lindsay, 1993) and the use of fire (Mentis & Bailey, 1990; Trollope *et al.*, 1995; van Wilgen *et al.*, 1998a; van Wilgen, Biggs & Potgieter, 1998b). The management of an area where 'natural' processes should be allowed to operate unimpeded has led to a number of concerns about the impacts of such management. These include a concern that the numbers of trees have declined over the past 50 years, putatively because of frequent fire and large numbers of elephant (van Wyk & Fairall, 1969; Coetzee *et al.*, 1979; Engelbrecht, 1979; Viljoen, 1988) and that the vegetation has become structurally more homogeneous due to regular prescribed burning at fixed intervals over large areas (van Wilgen *et al.*, 1998a,b). There is, however, little in the way of quantifiable data to justify these concerns.

The debate needs to be informed by means of good information on the dynamics of the savanna ecosystem. The major challenge to savanna community ecology has been to understand the mechanism of co-dominance between trees and grasses (Scholes, 1997). Disequilibrium theories, in which disturbance prevents competitive exclusion from proceeding to its logical conclusion, are often invoked to explain this co-dominance. The dominant forms of disturbance are fire and herbivory, which, together with irregularities in rainfall, are instrumental in shaping the structure of savanna vegetation. Fire, its role in the maintenance of savanna structure, and its use in management, is probably the oldest issue in savanna ecology (Scholes & Walker, 1993). In African savannas, mega-herbivores (Owen-Smith, 1988), and especially elephants, have a disproportionate effect on the structure of woody vegetation, although other species (such as porcupines, Yeaton, 1988) also play an important role. Many studies have implicated elephants in observed declines in woody vegetation (van Wyk & Fairall, 1969; Coetzee *et al.*, 1979; Engelbrecht, 1979; Pellew, 1983). Conversely, increases in the density of woody vegetation have been linked to declining numbers of elephants in many areas in Africa (Lock, 1993; Leuthold, 1996). Some studies have attempted to assess the interactions between fire and elephant utilization and damage in woodlands (Bell & Jachmann, 1984; McShane, 1987). These two factors, fire and elephants, have played an important role in shaping savanna ecosystems in Africa for many hundreds of thousands of years (Buechner & Dawkins, 1961; Agnew, 1968; Laws, 1970; Leuthold, 1977; Dublin, Sinclair & McGlade, 1990). An understanding of their role, especially with regard to the detection of acceptable limits of change, is essential for the sound management of conservation areas in Africa.

The fire history of the Kruger National Park is relatively well known (Trollope, 1993; van Wilgen *et al.*, 1998a), and has recently been captured on a geographical information system (van Wilgen *et al.*, 1998b). In addition, there are sets of aerial photographs dating back to 1940 which cover the whole park, and sets of fixed-point photographs which have been repeated regularly over the past two decades. The elephant population has also been monitored from the turn of the century. In this paper, we use these data to provide a first estimate of trends in woody vegetation cover and density in the Kruger National Park, and relate them, where possible, to the known history of fire and elephant densities.

Methods

Study site

The Kruger National Park is situated in the low-lying savannas of the eastern parts of the Northern and Mpumalanga Provinces of South Africa, adjacent to Mozambique in the east and Zimbabwe in the north. The park was established in 1926, and covers 1 948 528 ha. Elevations range from 260 to 839 m a.s.l. Mean annual rainfall varies from around 750 mm in the south to around 440 mm in the north, but variations around the mean can be marked from year to year (Tyson & Dyer, 1978). The park is crossed by six perennial rivers (the Crocodile, Sabie, Olifants, Letaba, Luvuvhu and Limpopo), which run from west to east. Geologically, the park can be divided into western and eastern halves. In the west, granites and their erosion products dominate, while the eastern sector is dominated by basalt, but includes the Lebombo Hills (primarily rhyolite formations) running from north to south. Two important areas of sandveld also occur in the north, around Punda Maria and Pafuri.

The known flora of the park comprises 1903 species, including over 400 tree and shrub species, and over 220 grasses. There are four major vegetation types in the park. In the south-west, the low nutrient status of the soils results in a relatively low grazing pressure, and grass fuels accumulate during the growing season; as a result fires tend to be relatively frequent (every 3 years on average) in these areas (Trollope, 1993). The area is well wooded, and important tree species include the red bushwillow (*Combretum apiculatum* Sond.), knobthorn (*Acacia nigrescens* Oliv.), tamboti (*Spirostachys africana* Sonder) and marula (*Sclerocarya birrea* [A. Rich.] Hochst.). In the south-east, on basalt substrates, grasses are more palatable and tend to be heavily grazed. Important tree species include the knobthorn, leadwood (*Combretum imberbe* Wawra) and marula. North of the Olifants River, the granite areas in the west are poorly grassed; mopane (*Colophospermum mopane* [Kirk ex benth.] Kirk ex J. Leonard) and red bushwillow are dominant trees. The north-eastern areas on basalt are dominated by multi-stemmed mopane shrubs about 1–2 m in height.

The fauna of the park is also diverse, including 147 species of mammals and 492 birds. Important herbivores include elephant (*Loxodonta africana* Blumenbach, 1797), buffalo (*Syncerus caffer* Sparrman, 1779), impala (*Aepyceros melampus* Lichtenstein, 1812), zebra (*Equus burchelli* Gray, 1824), wildebeest (*Connochaetes taurinus* Burchell, 1823), waterbuck (*Kobus ellipsiprymnus* Ogilby, 1833), kudu (*Tragelaphus strepsiceros* Pallas, 1766), giraffe (*Giraffa camelopardalis* Linnaeus, 1758), white and black rhinoceros (*Ceratotherium simum* Burchell, 1817 and *Diceros bicornis* Linnaeus, 1758) and hippopotamus (*Hippopotamus amphibius* Linnaeus, 1758). Herbivory, particularly by grazers, has an important impact on fires through the consumption of grass fuels. In addition, browsing (particularly by elephants) has a strong impact on subsequent tree mortality in fires. Numbers of large herbivore were low at the turn of the century, but built up steadily with protection. Elephant numbers have increased from zero in 1900 to around 7500 in 1967, when culling was instituted and their numbers subsequently allowed to fluctuate between 6500 and 8500 (Whyte & Wood, 1996).

The park has been subdivided into about 450 burning blocks to facilitate the programme of prescribed burning. The mean fire return periods on these blocks are known (van Wilgen *et al.*, 1998a) and were used in the interpretation of results from this study.

Approach

We used aerial photographs taken in the Kruger National Park in 1940, 1974 and 1998 to assess the density of woody vegetation at nine transects (Table 1). These transects are primarily situated in the southern-central part of the park, i.e. the area between the Sabie River in the south and the Olifants River in the north. The major landscapes covered are the Mixed *Combretum* spp./*Terminalia sericea* Woodland and *Sclerocarya birrea*/*Acacia nigrescens* Savanna (Gertenbach, 1983). The black and white photographs from 1940 and 1974 were scanned at a ground resolution of 45 cm, edited to make woody plants stand out clearly, and imported into the IDRISI GIS package for further analysis. The 1998 photographs were taken in digital format at a ground resolution of 45 cm. Aerial transects of approximately 1500×500 m were selected on each series of photographs. The aerial transects were selected so as to span two burning blocks of known fire history. This was done by selecting aerial transects divided by a road that marked the boundary between burning blocks. Within each aerial transect, cover values were estimated on 20 sample plots (approximately 135×90 m), of which ten were on each side of the road. Means were tested for significance using analysis of variance. The data were not normally distributed on basalt sites – in this case, tests were carried out on arcsine square-root transformed data.

In order to establish the accuracy of cover estimates made from aerial photographs, we also enumerated

Table 1 Salient features of nine transects selected to examine trends in woody vegetation cover in the Kruger National Park. Transects spanned two burning blocks. Fire return periods are given for each burning block where these differed

Transect number	Dominant geology	Fire return periods (years)	Years for which aerial photographs were examined
1	Granite	7.4	1940, 1974, 1998
2	Granite	7.4	1940, 1998
3	Granite	6.2; 7.4	1940, 1998
4	Granite	5.4; 4.3	1940, 1974, 1998
5	Granite	5.4	1940, 1998
6	Basalt	4.8; 6.2	1940, 1974, 1998
7	Basalt	11.7; 5.4	1940, 1974, 1998
8	Basalt	4.3; 7.4	1940, 1974, 1998
9	Basalt	7.8; 7.4	1940, 1998

woody vegetation cover on the ground. Sites were selected in the area where aerial transects were situated. At each of the nine sites, ten ground transects (10×50 m) were laid out, five on either side of the road. On each transect the canopy width and breadth of each shrub and tree >0.45 m tall were recorded. The estimated canopy cover on the transects was compared to the estimates of woody vegetation cover from the 1998 aerial survey. The graph was forced through the origin, because the coefficient for the intercept was not significant.

The relationship between fire return period and woody cover was examined using data from the fire monitoring programme (van Wilgen *et al.*, 1998a). Woody cover in 1998 was compared to these data using linear regression analysis. Again, arcsine square-root transformed data were used for basalt sites.

We also estimated rough trends in the density of trees in different height categories from a series of fixed-point photographs. These photographs were taken from marked locations in 1984 and again in 1996. We examined 44 pairs of photographs taken in granite areas and 44 pairs taken in basalt areas. On each photograph, the number of individual trees were counted in three height categories: <2 m, 2–5 m and >5 m. Data were log-transformed to correct for non-normal distribution, and were tested for significance using analysis of variance.

Results

Trends in the cover of woody vegetation

The initial cover (in 1944) of the woody vegetation was higher on granites than on basalts (Table 2). Over the past 50 years, the cover has increased on granites and decreased on basalts (Table 2). The trend was weaker and less consistent on granites, where no significant trends could be detected between 1974 and 1998. Overall, there has been a 12% increase in the estimated cover on granites, from 19.7% in 1940 to 22.1% in 1998. By constrast, the estimated cover on basalts has decreased

Table 2 Percentage cover of woody vegetation on nine transects in the Kruger National Park (see Table 1) determined from a series of aerial photographs spanning 58 years. A dash (–) indicates no estimate for the relevant year. Means with the same superscript do not differ significantly at $P < 0.05$ (analysis of variance)

	Date of aerial photography		
Transect number	1940	1974	1998
1	19.7	22.6	20.5
2	16.2	–	20.4
3	23.5	–	16.4
4	19.4	21.1	24.4
5	19.9	–	28.8
Mean for granite transects	19.7^{a}	21.8^{b}	22.1^{b}
6	13.4	12.3	9.4
7	11.3	9.2	4.8
8	14.8	5.7	3.6
9	8.1	–	3.6
Mean for basalt transects	11.9^{a}	9.1^{b}	4.3^{c}

by 64%, from 11.9% in 1940 to 4.3% in 1998. This trend was significant between the three periods examined, and was consistent on all transects.

Accuracy of cover estimates

Data from the ground surveys indicated a good correlation between estimates of woody cover made from aerial photographs and from ground surveys (Fig. 1). The correlation indicates that cover estimates made from aerial photographs can reliably be related to actual woody vegetation cover, and do not result from a misclassification of pixels in the scanned dataset.

The influence of fire frequency on woody vegetation cover

Fire return periods ranged from 3.5 to 17 years on the granite transects. There was a significant but weak relationship between woody cover and mean fire return period ($y = 19.54 + 0.46x$, where y is the percentage cover of woody vegetation, and x is the mean fire return period in years; $r^2 = 0.04$; $P = 0.022$). The situation was similar on basalt substrates, where mean fire return periods ranged from 4.2 to 17 years ($y = 3.96 + 0.22x$; $r^2 = 0.06$; $P = 0.017$). Predictably, woody vegetation cover declined as fires became more frequent, but the weak relationship suggests that other factors and interactions will need to be understood before these relationships can be used to explain the observed responses.

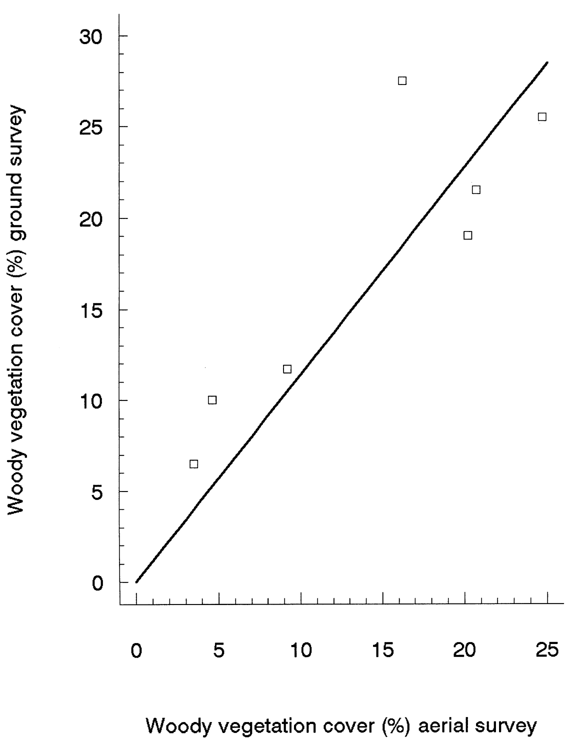

Fig 1 Relationship between estimates of woody vegetation cover from aerial photographs and from ground surveys. The relationship is $y = 1.14x$, where y is the percentage woody cover estimated from ground surveys, and x is the cover estimated from aerial photographs ($r^2 = 0.949$; $P < 0.001$). Data were adjusted to pass through the origin as the intercept was not significant.

Density and size class distribution of trees

The data from fixed-point photographs suggest that the observed decline in cover on basalts can largely be attributed to a decline in trees > 5 m high. These declined by 38% in the 12 years between 1984 and 1996, while the estimated density of smaller trees and shrubs (< 5 m) increased insignificantly on basalts (Table 3). The estimated density of large trees also decreased by 15% on granites, while the density of smaller trees and shrubs increased in line with the observed increases in cover (Table 3). The decrease in the density of the < 2 m category, albeit insignificant, will be explained later. It appears, therefore, that large trees have decreased on both dominant geological types.

Discussion

It is difficult to identify the possible causes for the trends detected in this study in the absence of an interactive ecosystem modelling framework. A range of factors (such as fire frequency and intensity, herbivore numbers, rainfall and soil fertility) would have driven these trends, and they need to be considered within such a framework, taking possible feedback loops into account. At this stage, therefore, any interpretations of the causes can only be speculative.

The indications that cover of woody vegetation has increased on granite substrates, but decreased on basalts, could be attributed to the dynamics of the vegetation in relation to soil properties (Knoop & Walker, 1985). Basalt substrates are relatively nutrient-rich, whereas those on granite are nutrient-poor. In times of drought, therefore, grazers remove much of the grass sward, and trees are benefited from the reduced competition from grasses (a typical bush-encroachment scenario associated with

Table 3 Changes in the density of trees (individual trees counted per photograph) in different height categories over 12 years in the Kruger National Park. Changes were assessed from 44 fixed-point photographs; significance levels were determined in an analysis of variance

Height class (m)	Geology	Year of photograph 1984	1996	Significance level
< 2	Basalt	14.0	17.2	$P = 0.054$
2–5	Basalt	10.1	12.2	$P = 0.13$
> 5	Basalt	4.7	2.9	$P = 0.005$
< 2	Granite	7.5	7.1	$P = 0.83$
2–5	Granite	3.5	4.0	$P = 0.03$
> 5	Granite	4.6	3.9	$P = 0.049$

many agricultural areas in African savannas). The same scenario, but even more prominent, is known to occur on private nature reserves and game farms to the west of the Kruger National Park (Zunckel & De Wet, 1994). This overgrazing may be the result of constant high herbivore numbers, in turn resulting from the artificial provision of water. Park officials also suspect that actual herbivore numbers may be higher than estimates from regular game counts due to an undercounting bias (Bothma, 1996). Although the density of grazing animals tends to be higher on basalts than on granites (W. S. W. Trollope, pers. comm.), grasses can recover from heavy grazing more rapidly on basalt substrates, because of the relative abundance of nutrients, and trees there have not benefited as much from reduced competition from grasses in these areas. Evidence for the rapid recovery of grasses on basalts, relative to granites, has been provided by the parks monitoring programme (Trollope, Potgieter & Zambatis, 1989), where recovery of grasses after drought on basalts was more rapid, and reached a higher biomass, than on granites (N. Zambatis, pers. comm.). Also, heavy grazing on the basalts may lead to higher run-off and evaporation (Knoop & Walker, 1985), which means less water becomes available to woody plants so that they gain only little or none at all from the reduced competition. The overall decrease in woody vegetation on basalt substrates can be related to frequent prescribed burning at fixed intervals for over 40 years (van Wilgen *et al.*, in press).

The decline in the numbers of large trees on both granite and basalt needs to be interpreted in relation to interactions between fire and utilization by elephants. The weak relationship between fire frequency and woody vegetation cover suggests that fire was not the only factor causing the decline, which was most marked in large trees. Elephants also have a marked impact on large trees. The elephant population in the Kruger National Park was estimated, using coarse techniques, to be around 1000 in 1960, although the number (given subsequent estimates) was probably around four times as high. In 1966, the first rigorous count produced an estimate of 6500, and numbers were maintained at around 7500 through culling since the early 1970s (Whyte & Wood, 1996). While mature trees can survive frequent fires in African savannas, utilization by elephants and other animals can damage trees and allow fires to burn exposed areas of wood (Yeaton, 1988). These scars tend to become larger with successive fires, and the trees eventually become structurally weakened and collapse. Frequent, regular fires (as practised in the park for the past few decades) would also serve to prevent smaller trees from developing into larger ones, especially in combination with browsing (Bond & van Wilgen, 1996). Thus, increased mortality and declining recruitment as a result of a combination of frequent, regular burning and increasing numbers of elephants appear to have resulted in an overall decline in the number of large trees.

The increase in the density and cover of lower woody plants on the granites can be ascribed to various other reasons. Although the < 2 m height category is mostly utilized by elephants (Guy in Thrash *et al.*, 1991), it is in fact this and the 2–5 m category which contribute to the increase in woody cover. According to Thrash *et al.* (1991), 'the destruction of trees by elephants is often followed by regrowth from the persistent root stocks'. The failure to detect any change in the density of < 2 m high woody vegetation (Table 3) could be due to recording lower number of individuals of this stratum, because the visibility has been obscured by woody plants standing in the foreground. This technique may therefore be unsuitable for detecting increases.

The above findings have implications for the management of the area (van Wilgen *et al.*, 1998b). The park's authorities have set thresholds of potential concern, which, if reached, should trigger an assessment of the causes and precipitate corrective action. One such threshold has been set, very widely, at an 80% change in the cover of any component of the vegetation in any given landscape. Thus, the 64% change in woody cover detected here, with indications that the trend will continue, is rapidly approaching one of the defined thresholds. The most obvious steps to counter these trends would be the closure of at least some of the artificial water points, and changes to the fire management policy away from regular burning at frequent intervals. Such measures are already implemented, with the closure of water points commencing in 1994 and a lightning fire approach being introduced in 1993 (Trollope *et al.*, 1995; van Wilgen *et al.*, 1998). It is of the utmost importance that additional data sets be analysed and interpreted, also for other parts of the park, to substantiate the current trend.

Acknowledgements

We thank Tony Palmer, Rina Grant, Winston Trollope, Mike Peel and Nick Zambatis for useful guidance in the analysis and interpretation of the data. Sean O'Regan and Richard Sowry are thanked for the field work they conducted and the data they generated. B.v.W. thanks the CSIR Division of Water, Environment and Forestry Technology, and South African National Parks for supporting this work.

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(Manuscript accepted 5 June 1999)