

Fire, Grazing and the Dynamics of Tall-Grass Savannas in the Kalakad-Mundanthurai Tiger Reserve, South India

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Abstract: *Prescribed burning is often used to enhance forage availability for herbivores in rangelands worldwide. This study evaluated the utility of such prescribed burning as a management tool to improve herbivore habitat quality in the Mundanthurai plateau region of the Kalakad-Mundanthurai Tiger Reserve (KMTR), south India. Currently, large tracts of the plateau are dominated by the unpalatable tall-grass species *Cymbopogon flexuosus*, and populations of mammalian herbivores and predators in the region are low. Responses of *C. flexuosus* communities to experimentally-imposed fire and grazing regimes were studied, and the effectiveness of fire in suppressing this tall-grass species assessed.*

*Two years following burning, *C. flexuosus* cover in burnt plots was indistinguishable from unburned sites, suggesting that *C. flexuosus* individuals are fairly stable against perturbations by fire. On the other hand, clipping experiments which simulated a scenario of high intensity grazing indicate that *C. flexuosus* fares poorly under sustained grazing, suggesting the potential for grazer-control of this species. However, *C. flexuosus* is typically avoided by grazers except for short periods following burning. Although grazing in these communities was higher post-burn responses of plots experiencing 'natural' levels of grazing indicate that grazer densities at KMTR are presently*

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too low to prevent *C. flexuosus* from quickly re-attaining competitive dominance following burning. Under the current conditions of low herbivore densities, prescribed burning, by itself, is therefore unlikely to significantly improve herbivore habitat in KMTR. For burning to be effective, it must be coupled with other parallel management strategies aimed at augmenting grazer densities in the reserve.

Keywords: fire, grazing, savanna, tall-grass species, Kalakad-Mundanthurai Tiger Reserve, *Cymbopogon flexuosus*.

INTRODUCTION

PROTECTED AREAS in India are subject to a host of different pressures that stem from the increasing demands of a growing human population. In most areas, these pressures include disturbances such as fire, collection of firewood and other forest produce, logging, and illegal grazing of cattle within reserve boundaries. Where they occur, such disturbances have the potential to create a cascade of ecological changes, from the level of species to that of the ecosystem.

The Kalakad-Mundanthurai Tiger Reserve (KMTR) in southern India is no exception, currently experiencing escalating pressure from the local populace that depends on a range of forest products for a living (Ali and Pai 2001; Dutt 2001; Melkhani 2001). Located at the southern end of the Western Ghats, a global biodiversity 'hotspot' (Myers et al. 2000), the reserve is home to a diverse array of plant and animal species including several endangered species such as tigers (*Panthera tigris*), leopards (*Panthera pardus*), elephants (*Elephas maximus*), gaur (*Bos gaurus*), lion-tailed macaques (*Macaca silenus*) and Nilgiri tahr (*Hermitragus hylocrius*; Johnsingh 2001). In addition, it is recognised as a centre of high plant diversity in India (Ganesh et al. 1996) and also represents the southernmost range of the tiger in India, making it an area of high conservation priority (Johnsingh 2001). Although the area was declared a Tiger Reserve in 1988 and has a long history of protection, the reserve has nevertheless experienced significant ecological changes over the years (Ramesh et al. 1997; Ramakrishnan et al. 1999; Sankaran 2001a, 2001b).

Between 1960 and 1990, forested habitats in the region were lost to plantations, reservoirs, and human encroachments at a rate of almost 0.33% annually (Ramesh et al. 1997). Overall forest-loss rates have since declined (Sankaran 2001b), but several areas of the reserve, particularly along the eastern border and around human enclaves within the reserve, remain under threat of deterioration from anthropogenic activities (Ali and Pai 2001; Sankaran 2001a, 2001b). In addition, KMTR has also witnessed changes in its plant and animal communities in recent years (Ramakrishnan et al. 1999; Sankaran 2001a). Of

particular concern with respect to the site's designation as a tiger reserve is the fact that populations of large herbivores and predators in the region are currently low (Viswanathan 1996; Ramakrishnan et al. 1999; Johnsingh 2001; Sankaran 2001a). Declines in herbivore populations have been particularly pronounced in the Mundanthurai plateau region of KMTR, an area of approximately 60 km² at an elevation of about 200 msl, and the focal area for this study. Of the major terrestrial herbivores that co-exist in the Mundanthurai plateau, reductions have been most conspicuous in the case of spotted deer or *chital* (*Axis axis*), from an estimated 200 within the 60 km² of the plateau in 1984 (Johnsingh and Sankar 1991) to levels too low in 1995 to permit accurate density estimation (Viswanathan 1996). As of 1999, total herbivore biomass density in the area was ~ 1064 kg/km², with more than half of the biomass accounted for by domestic livestock (Sankaran 2001a). Herbivore densities, particularly *chital*, are amongst the lowest recorded within protected areas in Asia supporting similar species complements (Table 1). Quantitative data on predator populations in the Mundanthurai plateau are lacking. However, scat analyses indicate that densities of leopards (*Panthera pardus*) are about half that found in other protected areas such as Mudumalai Wildlife Sanctuary (Ramakrishnan et al. 1999), while few, if any, tigers (*Panthera tigris*) frequent the plateau (Ramakrishnan et al. 1999; *pers. obs.*).

A low density of mammalian herbivores, especially *chital*, is of significant management concern since this species forms a major part of the prey-base for higher level predators (Karanth and Sunquist 1995). Although the reasons underlying such low herbivore and predator densities in the Mundanthurai plateau remain unclear, the current widespread dominance of unpalatable tall-grass species in the area suggests that lack of suitable food plants might be a potential factor contributing to low herbivore densities, and in turn low predator densities. Currently, a sizeable portion (~ 22%, M. Sankaran *unpubl. data*) of the Mundanthurai plateau comprises savanna-grasslands dominated by the native tall-grass species *Cymbopogon flexuosus*: a fire-tolerant, fast-growing species which contains a variety of aromatic compounds in its tissues that act as deterrents to herbivores except when plants are immature or immediately following burning. Consequently, large sections of the plateau presently comprise poor quality habitat for herbivores. Although quantitative data are lacking, anecdotal reports suggest that this widespread dominance of unpalatable tall-grasses is a recent phenomenon; large sections of the plateau remained relatively open until the late 1980s-early 1990s, supporting higher herbivore numbers than today (R. Ali *pers. comm.*, A. J. T. Johnsingh *pers. comm.* and K. Sankar, *pers. comm.*).

Table 1
*Densities (number. km⁻²) of the dominant native ungulates in the Mundanthurai plateau, chital (*Axis axis*) and sambar (*Cervus unicolor*), as compared with other protected areas in the Indian subcontinent*

Locality	Habitat	Chital	Sambar	Source
Pench Tiger Reserve	Dry deciduous forest	80.7	6.1	Biswas and Sankar 2002
Gir National Park	Dry deciduous forest	57.3	3.5	Khan et al. 1996
Nagarhole National Park	Dry and moist deciduous forest	50.6	5.5	Karanth and Sunquist 1992
Kanha National Park	Moist deciduous forest	49.7	1.5	Karanth and Nichols 1998
Sariska Tiger Reserve	Dry deciduous forest	30.7 – 76.8	10.8 - 15	Sankar 1994
Ranthambhore Tiger Reserve	Dry deciduous forest	31	17.1	Bagchi et al. 2004a
Mudumalai Wildlife Sanctuary	Dry deciduous forest	25.03	6.61	Varman and Sukumar 1995
Bandipur National Park	Dry deciduous forest	20.1	5.6	Jathanna et al. 2003
Bhadra Tiger Reserve	Moist deciduous – bamboo forest	2.8 – 4.5	0.89 – 4.5	Ahrestani 1999; Jathanna et al. 2003
Mundanthurai plateau, KMTR	Savanna – Dry deciduous forest	1.87	2.78	Sankaran 2001a

The reasons underlying the current widespread dominance of the tall-grass species *C. flexuosus* in the Mundanthurai Plateau are unknown. What is clear, however, is that there is an urgent need for management interventions to improve forage availability for ungulates and thereby augment herbivore populations in the reserve. Previous research at KMTR has similarly stressed the need for such interventions (Johnsingh 1986; Johnsingh and Sankar 1991; Ramakrishnan et al. 1999; Dutt 2001), with appropriate fire management proposed as a means to this end (Johnsingh 1986, 2001; Dutt 2001). Fire is a common occurrence in savannas and grasslands worldwide, and has long been used as a tool in ecosystem management (Bowman 1998; Freckleton 2004). For example, burning was historically employed by the aboriginal people of Australia to provide favourable habitats for herbivores and to increase the abundance of food plants (Bowman 1998), and it continues to be used as a tool to manage grasslands for grazing by large ungulates in many of the world's rangelands and protected areas (Moe and Wegge 1997;

Freckleton 2004). Given the well-documented preference of wild ungulates for burned areas (Wilsey 1996; Moe and Wegge 1997; Fuhlendorf and Engle 2004), it seems likely that a strategy of prescribed burning will benefit ungulate conservation in the Mundanthurai plateau by enhancing forage availability for grazers. Nevertheless, in order to assess the efficacy of such a management strategy in KMTR, we need a better understanding of how fires and grazing interact to influence the dynamics of plant communities, particularly tall-grass savannas, in the reserve. However, there have been no quantitative studies that have evaluated such effects in the reserve thus far.

This paper reports results from an experimental study aimed at investigating the individual and interactive effects of fires and mammalian grazing on savanna-grassland plant community composition and diversity at KMTR. A primary objective of the study was to examine the responses of unpalatable tall-grass species to these perturbations, and thereby evaluate the effectiveness of fire as a tool to control tall-grasses and improve herbivore habitat quality in the reserve.

STUDY AREA AND METHODS

The study was conducted between 1997 and 1999 at the Kalakad-Mundanthurai Tiger Reserve, India (KMTR; 8°25'-8°50'N, 77°15'-77°40'E). The site was designated a Tiger Reserve in 1988 following the merger of two previously protected areas, the Kalakad Wildlife Sanctuary (established in 1971) and the Mundanthurai Wildlife Sanctuary (established in 1962; Johnsingh 2001). The reserve presently covers an area of approximately 900 km² and spans an altitudinal gradient from about 100 m – 1867 m. The diverse topography of the reserve, coupled with spatially varying climatic and edaphic factors, results in the occurrence of a host of different vegetation types (Ganesh et al. 1996), purported to be among the largest range of habitats within any protected area in peninsular India (Ali 1999). KMTR and the surrounding Agasthyamalai region harbour about 2000 of the 3500 plant species that occur in the Western Ghats, 7.5% of which are local endemics (Ganesh et al. 1996). The faunal component of the reserve comprises at least 273 bird, 81 reptile, 37 amphibian, 33 fish and 77 mammal species (Johnsingh 2001 and references therein).

The focal area for the study, the Mundanthurai plateau, is an area of approximately 60 km² at an elevation of about 200 msl. Mean temperatures here fluctuate between 17°C and 37°C annually. Yearly rainfall averages about 1189 mm (Johnsingh and Joshua 1994). Dry deciduous forests, plantations, and thorn scrub forests collectively comprise the most prevalent habitat type in the plateau, covering about 50% of the study area. Savanna habitats dominated by the tall-grass species *Cymbopogon flexuosus* account for 22% of the study area, riverine forests and moist deciduous forests about 16.5%, short grasslands and other open habitats 9% and water bodies the remaining 2.5% (Sankaran 2001a). The terrestrial mammalian herbivore community in the study area comprises 4 native species: sambar deer (*Cervus unicolor*), chital or spotted deer (*Axis axis*), black-naped hare (*Lepus nigricollis*) and Indian chevrotain or mouse deer (*Tragulus meminna*).

In addition, domestic livestock including buffalo (*Bubalus bubalis*) and cattle (*Bos indicus*) also graze there. Detailed descriptions of the study area can be found in Johnsingh and Sankar (1991) and Johnsingh and Joshua (1994).

Although the management has adopted a policy of fire suppression in the reserve (Anon. 1978), fires of anthropogenic origin are nevertheless common occurrences in KMTR (*pers. obs.*). In fact, as of 1989, KMTR showed some of the highest recorded incidence of fires within sanctuaries and national parks in India (Kothari et al. 1989), with an estimated 3% of the reserve area and 6% of savanna habitats possibly more burning annually by the late 1990s (Sankaran 2001a, b). Accidental fires and illegal burning for fresh forage are the primary causes of most fires (Johnsingh 1986; *pers. obs.*), which are typically restricted to grassland and savanna habitats in the reserve (Sankaran 2001a, b). Several grasslands in the reserve, particularly those along steep hill-sides, burn on an annual basis. Within the Mundanthurai plateau, where protection measures are more stringent, fire return periods > 3 years are not uncommon (*pers. obs.*).

Methods

Three different sites, dominated by the unpalatable tall-grass species *Cymbopogon flexuosus*, were selected for this study. These sites had not burned for at least 3 years prior to the start of the experiment. The experimental design was a 3x3 factorial experiment involving 3 burning treatments (unburned, burnt once a year, burnt once in 2 years) and 3 grazing treatments (ungrazed, grazed, and experimentally clipped). The experimentally clipped treatments were used to simulate high levels of grazing, as might have occurred in the past. At each site, a 15x15 m area was demarcated consisting of a square grid of nine 4x4m plots with a 1m gap between plots and a 50cm walk-way around the edge. Six plots at each site were fenced to exclude herbivores. Each of the 9 plots at a site was assigned one of 9 burning x grazing treatments in a constrained random fashion (i.e. the fenced area included the ungrazed and experimentally clipped treatments). All experimental burns were conducted at the start of the dry season in March 1997. A further subset of these was burned again in March 1998. In plots assigned clipping treatments to simulate high-intensity grazing, all vegetation was clipped down to about 5 cm every 15 to 30 days depending on growth.

Plots were sampled prior to experimental treatments, and periodically afterward for a period of 2 years. At each sampling period, the number of different plant species present in plots (species richness S) was quantified. In addition, the percent canopy cover of different species and the total live herbaceous cover in plots were also estimated. Within each 4x4 m plot, cover of individual species was estimated in four 1m² subplots using a systematic sub-sampling scheme. Species cover was estimated visually using a 1x1 m grid-frame subdivided into hundred 0.01 m² units.

Data were analysed to determine how different burning and grazing treatments influenced the cover of the tall-grass species *C. flexuosus* in plots. In addition, the

effects of experimental burning and grazing treatments on the plant community as a whole were also analysed based on 3 different indices: plant species richness (S), evenness (J) and diversity (H'). Species richness is just the number of different plant species present in plots. Species evenness or equitability (J) is a measure of the relative abundance of different species in a plot. For a given species richness, evenness is highest when all species are equally abundant in plots, and low when one or a few species are dominant and others rare. Species diversity (H') combines aspects of richness (S) and evenness (J). For a given richness, a community with a high evenness (J) is considered to be more diverse than one with low evenness.

Species diversity was quantified using the Shannon-Weaver index

$$H' = -\sum p_i * \ln(p_i)$$

where p_i represents the relative contribution of the i^{th} species to the canopy.

Species evenness or equitability was determined as

$$J = H' / \ln(S)$$

where S represents species richness.

During the first year of the study, data were also collected on the number of plants that were grazed in unfenced plots. In addition, at the start of the experiment, three soil samples (5x5x5 cm) were collected from each *C. flexuosus* plot assigned a burning treatment, and germinated to quantify soil seed banks. For comparative purposes, an equal number of samples ($N = 18$) were collected and germinated from adjacent high diversity communities that were not dominated by *C. flexuosus*. Soils were germinated in a greenhouse in 20 cm tall circular polythene bags of approximately 10 cm diameter, which were watered (75 ml) every 2 to 3 days and germination success recorded every 2 weeks for 12 weeks. Although the germination experiment was part of another ongoing study at the site (Sankaran 2001a), results are reported here because of their relevance to the present study.

Data were analysed as an ANOVA for a 2-way factorial experiment in a completely randomised block design using the statistical program R (<http://www.r-project.org/>). Where main effects were significant, treatment means were compared using Tukey's Honestly Significant Difference (HSD) multiple comparison test. All data were tested for deviation from normality and homogeneity of variances, and did not require transformation prior to analysis. Results reported here are from 1999, two years following the start of experimental manipulations.

RESULTS

At the start of the study, all plots were similar in terms of total herbaceous cover, cover of *C. flexuosus*, species richness (S), diversity (H'), and evenness (J; $p > 0.05$ for all main effects and interaction terms). Mean live herbaceous cover in plots was approximately 63%, of which ~78% was accounted for by the unpalatable tall-

grass species *C. flexuosus*. Prior to experimental manipulations, species richness (S), diversity (H'), and evenness (J) of plots (16m²) averaged 24 ± 1.9, 2.2 ± 0.06 and 1.9 ± 0.04, respectively (values following means are 1 standard error).

No significant interaction between burning and grazing treatments were detected at the end of 2 years for any of the response variables considered (Table 2). In other words, plant communities showed qualitatively similar responses to different burning treatments at the end of 2 years whether or not they were grazed, ungrazed, or experimentally clipped. Likewise, different grazing treatments elicited similar responses for all burning treatments. The effects of burning and grazing on plant community dynamics are therefore discussed separately below.

Table 2

Results of the randomised complete block design ANOVAs for the factorial experiment showing the main effects and 2-way interaction for different response variables

Effect	d.f.	Total cover		<i>C. flexuosus</i> cover		Richness (S)		Diversity (H')		Evenness (J)	
		F	P	F	P	F	P	F	P	F	P
Burning	2, 16	18.11	<0.001	0.28	0.75	3.53	0.054	1.13	0.35	0.95	0.41
Grazing	2, 16	33.23	<0.001	33.74	<0.001	19.5	<0.001	10.3	0.001	8.23	0.003
Burning x Grazing	4, 16	2.58	0.07	2.64	0.07	1.0	0.44	0.68	0.62	0.71	0.60

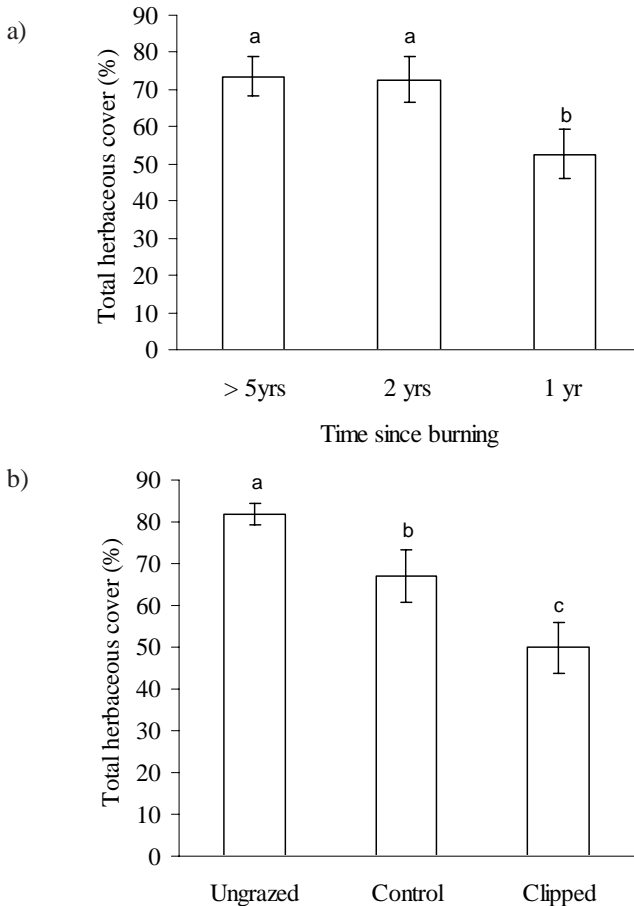
Note: Data are from 2 years following the start of experimental manipulations. Significant terms are displayed in bold

Effects of Burning Treatments

At the end of 2 years, there were significant differences between plots assigned different burning treatments (Table 2, Figure 1a). Not surprisingly, annual burning significantly lowered total live herbaceous cover in plots (Figure 1a). One year following burning, total herbaceous cover in plots assigned the annual burning treatment was significantly lower than in plots burnt 2 years previously or left unburned (Figure 1a). However, within 2 years following burning, live herbaceous cover in burnt plots was indistinguishable from plots that had not burned in more than 5 years (Figure 1a). Importantly, none of the burning treatments had any significant effect on the cover of the tall-grass species *C. flexuosus* in plots (Table 2), suggesting that this species is highly resistant to fire.

Burning resulted in a short-term (2-4 months) decrease in plant species richness (S), evenness (J) and diversity (J') of plots (data not shown). However, such effects were transient and within a year following burning, species richness

Figure 1
Effect of different burning (a) and grazing treatments (b) on total herbaceous cover in plots



Notes: Data are from 2 years following the start of the experiment. Effects of fire on total herbaceous cover are plotted in terms of time since the last burn which is > 5 yrs for unburned plots, 2 years for biennially burnt plots and 1 yr for annually burnt plots. Bars represent means (± 1 S. E.) of 9 replicate plots within each treatment. Different letters above bars represent significant differences between treatment means according to Tukey's HSD multiple comparison tests (joint $\alpha = 0.05$).

and diversity of burnt plots had recovered to match those of unburned plots. At the end of the study, there were no significant differences in plant species richness (S), diversity (H') or evenness (J) between plots that were left unburned or those that had been burnt one or two years previously (Table 2). *C. flexuosus* communities in KMTR, therefore, appear to be highly stable to perturbations by fire, rapidly returning to their pre-burn states following burning.

Effects of Grazing Treatments

Grazing treatments had a significant effect on all of the response variables considered (Table 2). Within 2 years following fence construction, total live herbaceous cover increased by an average of 15% in ungrazed plots (Figure 1b). Simulated high-intensity grazing through periodic clipping decreased herbaceous cover by ~17% in plots (Figure 1b). Grazing treatments, however, had a disproportionate effect on the cover of the tall-grass *C. flexuosus* (Figure 2a), with *C. flexuosus* individuals faring particularly poorly under sustained levels of grazing. The cover of *C. flexuosus* increased by 17% in fenced plots and decreased by 27% in clipped plots (Figure 2a). Further, reduction in cover of *C. flexuosus* individuals in clipped plots (Figure 2a) was not balanced by compensatory increases in live cover of other species (Figure 1b), and clipping resulted in a net decrease in total herbaceous cover and a net increase in the amount of bare ground present in plots (Figure 2b). The lack of compensatory responses by other species results, in part, from depressed seed germination in *C. flexuosus* communities, which was almost an order of magnitude lower than in adjacent grasslands (Figure 3). At present, it is unclear whether such depressed germination is a consequence of impoverished soil seed banks or due to other factors such as allelopathy, and whether, given sufficient time, other species would adequately compensate for loss of *C. flexuosus* cover when intensively grazed.

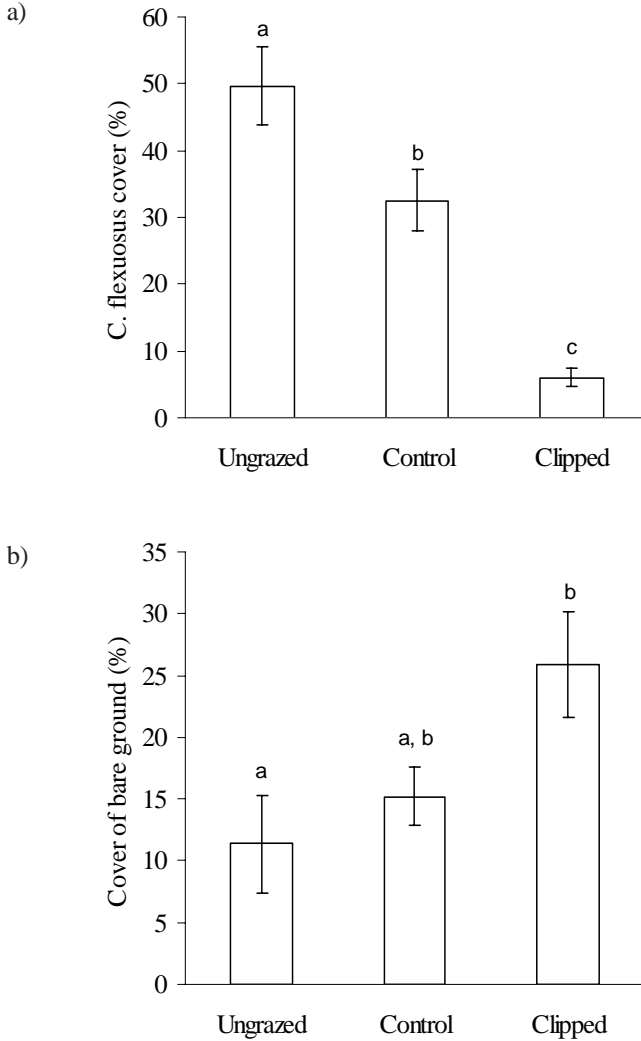
Grazing also significantly influenced species richness and diversity of plots (Figure 4). Plant species richness (S), diversity (H') and evenness (J) were significantly lower in ungrazed plots compared to those that were clipped or sustained 'natural' levels of grazing (Figure 4, Table 2). When ungrazed, *C. flexuosus* increased in dominance (Figure 2a), out-competed subdominant species and lowered richness, evenness and diversity (Figure 4). Grazing and clipping prevented *C. flexuosus* from attaining levels of dominance seen in ungrazed plots (Figure 2a), which permitted subdominant species to persist and resulted in higher species richness, evenness and diversity in plots. Compared to plots exposed to natural levels of grazing, clipping resulted in a marginal, but non-significant, increase in all three variables (Figure 4, Table 2), suggesting that high-intensity grazing can potentially lead to higher plant species diversity in these tall-grass communities.

Short Term Interactive Effects of Burning and Grazing on C. flexuosus

Although responses of *C. flexuosus* individuals to grazing treatments at the end of 2 years were not influenced by burning (non-significant 2-way interaction, Table 2), over shorter time scales (up to 4 months) burning resulted in a 5-fold increase in the number of *C. flexuosus* plants grazed in plots (Figure 5). However, these effects were transitory, and grazing on *C. flexuosus* individuals returned to negligible levels within a year post-burn.

Figure 2

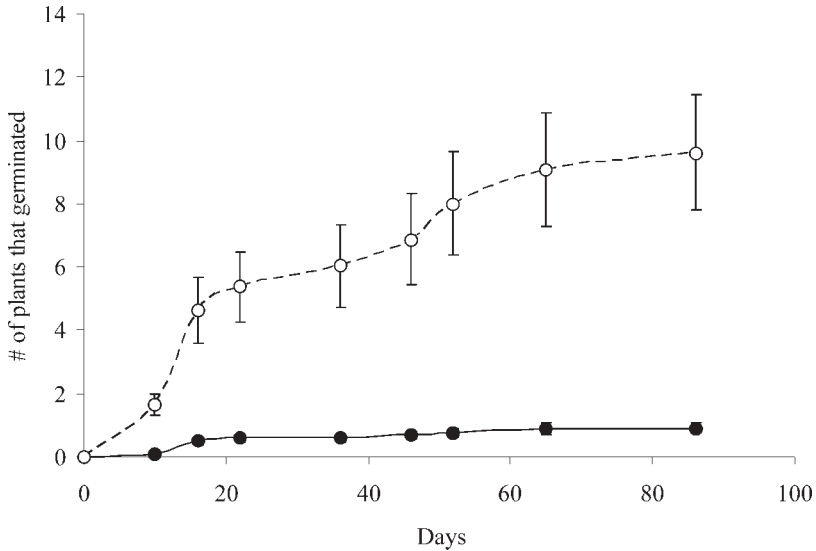
Effect of different grazing treatments on the (a) cover of the tall-grass species, *C. flexuosus*, and (b) cover of bare ground in plots



Notes: Bars represent means (± 1 S. E.) of 9 replicate plots within each treatment. Different letters above bars represent significant differences between treatment means according to Tukey's HSD multiple comparison tests (joint $\alpha = 0.05$).

Figure 3

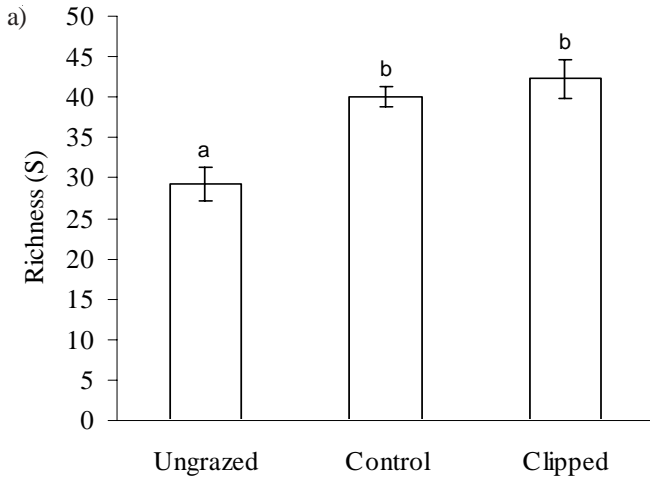
A comparison of germination patterns over time from soil cores collected from experimental plots dominated by the tall-grass species *C. flexuosus* (filled circles) and adjacent sites that did not contain *C. flexuosus* (open circles)

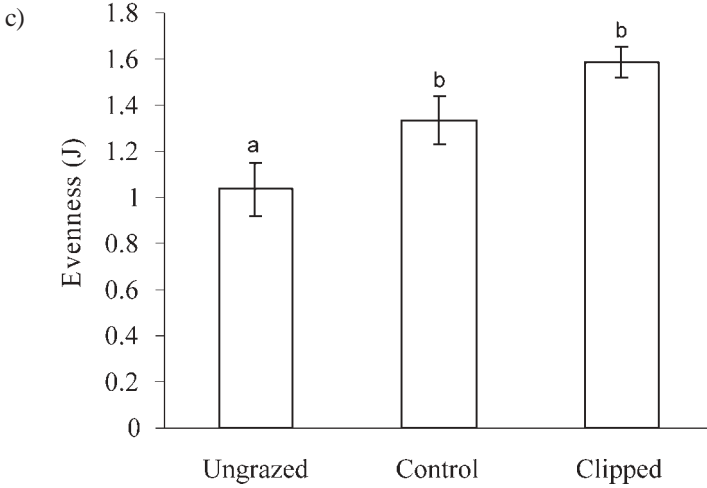
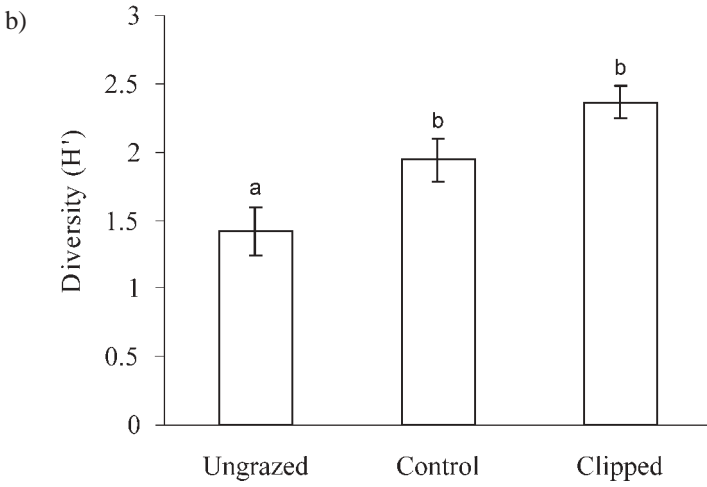


Notes: Values are averaged across 18 replicate 5×5×5cm soil samples for both community types. Bars represent ± 1 standard error.

Figure 4

Effect of different grazing treatments on (a) plant species richness (*S*), (b) species diversity (*H'*) and (c) species evenness (*J*) in plots

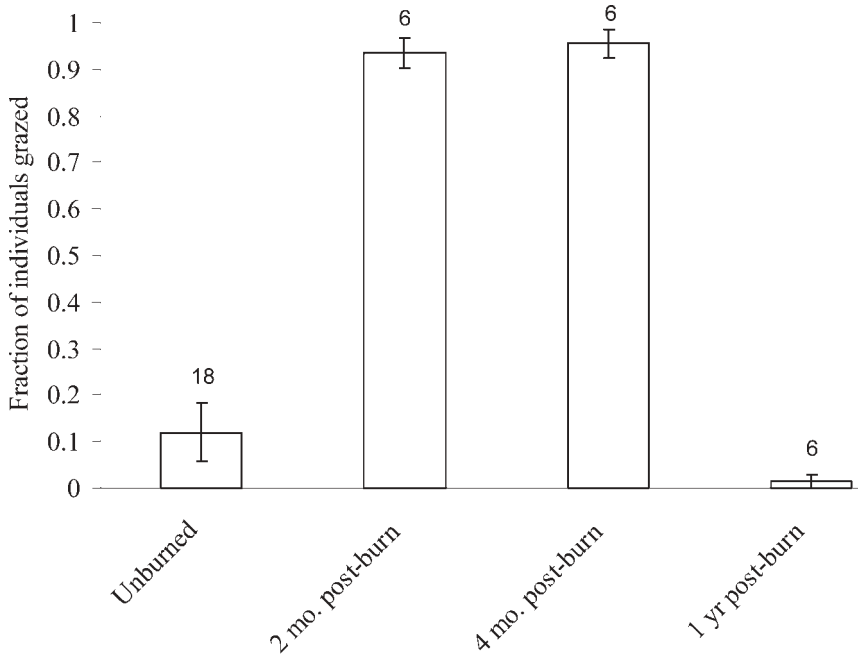




Notes: Bars represent means (\pm 1 S. E.) of 9 replicate plots within each treatment. Different letters above bars represent significant differences between treatment means according to Tukey's HSD multiple comparison tests ($\alpha = 0.05$).

Figure 5

Herbivore utilisation patterns of *C. flexuosus*, as indexed by the proportion of individuals grazed, in unburned plots and over time in burnt plots



Notes: Bars represent ± 1 standard error. Values for burned plots (2 months, 4 months and 1 year post-burn) are based on data from 6 replicate treatment plots at each time period. Values for unburned plots include data from all plots prior to experimental manipulations and from 3 unburned plots from 3 different sampling periods.

DISCUSSION

The primary objective of this study was to investigate how fires and grazing influenced plant community dynamics in *C. flexuosus* dominated savanna grassland communities in the Mundanthurai plateau region of KMTR, and thereby evaluate the utility of fire as a tool in managing these habitats for herbivores. Although historically believed to be covered by deciduous forests, large sections of the plateau were clear-cut in 1966 for plantations that failed for various reasons (Johnsingh 1986, 2001). The area subsequently came to be referred to as the 'deer-valley' based on heavy use by *chital* (*Axis axis*) and other herbivores, notably domestic livestock (Johnsingh 1986). Currently large tracts of the plateau, including

'deer-valley', are dominated by tall-grass savannas and thorn-scrub woodlands, which is of particular management concern since they represent poor quality habitat for herbivores.

The results of this study have important implications for the management of *C. flexuosus* dominated savanna grassland communities in the region. First, results from the small scale experiments conducted here suggest that under the current conditions of low herbivore densities, burning, by itself, is unlikely to be an effective tool for improving herbivore habitat quality by reducing cover of unpalatable tall-grasses in these communities. *C. flexuosus* is a fire tolerant, fast growing species that is capable of quickly attaining competitive dominance in the post-fire environment through rapid regrowth from belowground carbon stocks. Where grazing pressure is low, as is the case in KMTR, these communities are fairly stable to perturbations by fire. Burning had no effect on the cover of *C. flexuosus* individuals (Table 2) and within 2 years of burning, total live herbaceous cover in burnt plots was indistinguishable from unburned plots (Figure 1A). Previous work has demonstrated that these communities also display a high degree of compositional stability in response to burning (Sankaran and McNaughton 1999). The relative abundance of different species did not change significantly following burning (Sankaran and McNaughton 1999), indicating that fire by itself is unlikely to induce compositional shifts favouring more palatable species.

In contrast, results from the clipping experiments suggest the potential for significant grazer control of species composition in these communities, as *C. flexuosus* individuals do not fare well under sustained levels of grazing (Figure 2A). However, herbivore usage of *C. flexuosus* savannas tends to be restricted to short periods immediately following burning (2–4 months; Figure 5); *C. flexuosus* communities are sparingly used by herbivores when mature or unburned, since they provide little in terms of palatable forage (Figure 5). Any measure of control that herbivores are capable of exerting on this species is, therefore, likely to occur only during periods immediately following burning. Herbivore avoidance of mature communities dominated by members of the genus *Cymbopogon* has also been observed in other ecosystems such as the Serengeti National Park, Tanzania (McNaughton 1983). In fact, for East Africa, Vesey-Fitzgerald (1973) reported that herbivores were capable of successfully suppressing *Cymbopogon* species when these communities were burnt. Similar results were not evident at KMTR. Even though herbivore utilisation of *C. flexuosus* grasslands was higher immediately following burning, such effects were short-lived (up to 4 months). Presumably, grazing pressure on the experimental plots was too low to prevent this species from quickly re-attaining competitive dominance, rendering these habitats unsuitable for herbivores within a year (Figure 5). Furthermore, surveys of vegetation recovery in *C. flexuosus* grasslands following larger 'natural' fires in the plateau indicate a similar pattern (Sankaran, *unpubl. data*), suggesting that the observed trends are not merely an artifact of the small plot sizes employed for the experiment.

If patterns observed at these small scales also hold at larger scales, prescribed burning of these habitats, by itself, will not represent a fruitful herbivore

management strategy at the current time. For burning to be effective, it must be coupled with other parallel management strategies for reasons detailed below:

- i) Any effect that burning is likely to have on species composition in tall-grass *C. flexuosus* communities will potentially arise from indirect effects through changes in the post-fire grazing environment, rather than through any direct effects such as mortality or local extinction-colonisation dynamics. Currently, herbivore densities in the reserve appear too low to exert any sort of control on *C. flexuosus* individuals in burnt patches and, hence, alternate measures to augment herbivore populations need to be explored. These could include animal re-introductions and the creation of additional grazing meadows in adjacent habitats such as thorn-scrub forests (Johnsingh and Sankar 1991; Johnsingh 2001) through undergrowth clearance and small clear-cuts (Dutt 2001).
- ii) Observations from experimentally clipped *C. flexuosus* plots (Figure 2B), and results from germination experiments (Figure 3), indicate that although aboveground biomass of *C. flexuosus* individuals may be drastically reduced following clipping or sustained grazing, colonisation of these plots by other species is extremely slow for one reason or another, resulting in large patches of bare ground in these communities. These results suggest that management strategies might need to also consider approaches such as seeding burnt areas with palatable species to improve forage availability for herbivores in these habitats.
- iii) Data from experiments reported here as well as field observations made during the course of the study indicate that grazing on *C. flexuosus* individuals is higher immediately following burning. However, data on consumption by different herbivore species in the post-burn environment are currently lacking. Typically, larger-bodied herbivores tend to be generalist feeders capable of tolerating lower quality food while smaller-bodied ones are more selective in their diet, requiring food plants that are of higher quality (Demment and Van Soest 1985). Limited observations made during the course of the study indicate that large bodied herbivores such as domestic buffalo (*Bubalus bubalis*)—which illegally graze the study area—are the predominant consumers of the low quality forage provided by *C. flexuosus*. Field studies or cafeteria trials are urgently needed to assess consumption of post-fire *C. flexuosus* regrowth forage by smaller-bodied native ungulates, particularly *chital*. If consumption of *C. flexuosus* by native grazers is negligible even following burning, then managers will need to consider alternate avenues such as the re-introduction of controlled rotational grazing by domestic buffalo, or tall-grass suppression through directed harvesting of *C. flexuosus* for its essential oils (Ali 1999), in order to improve habitat quality for native grazers.

One option available to the management is to let the plateau succeed to thorn scrub woodlands and eventually back to dry-deciduous forest. However, such a strategy might conceivably result in a further lowering of herbivore densities, particularly *chital*, in the early phases of the succession sequence, given their propensity to avoid tall-grass habitats and thorn-scrub woodlands in the plateau (Sankaran 2001a). Besides rendering herbivore populations more susceptible to local extinctions, such effects are also likely to have adverse impacts on the predator community at KMTR. Further, such an approach is at odds with one of the primary management objectives of Project Tiger which aims to maintain viable populations of both predators and their prey (Dutt 2001). A more pro-active approach to augmenting habitat suitability for herbivores, coupled with judicious fire management, must be adopted if stable herbivore and predator populations are to be maintained in the reserve.

Of particular relevance for herbivore conservation in the Mundanthurai plateau is the need for quantitative studies that document the role of competitive versus facilitative interactions, specifically between domestic and native ungulates, in structuring the herbivore community in Mundanthurai. Competition between livestock and wild herbivores, as demonstrated by increases in wild herbivore populations following livestock removal or differences in wild herbivore densities between livestock-grazed and livestock-free areas, has been previously reported from other ecosystems both in India (e.g., Gir National Park, Khan et al. 1996; Bandipur National Park and Tiger Reserve, Madhusudan 2004; trans-Himalaya, Bagchi et al. 2004b; Mishra et al. 2004) and elsewhere (e.g. Ngorongoro Crater, Runyoro et al. 1995). In these systems, livestock competed most strongly with native herbivores that were similar in size and feeding strategy (Bagchi et al. 2004b; Madhusudan 2004), with removal of livestock particularly favouring these species. In the Mundanthurai plateau, however, there are no native herbivores similar in size and feeding strategy to domestic cattle and buffalo, gaur (*Bos gaurus*) being restricted to higher elevations in the reserve. Consequently, removal of livestock from the plateau would potentially result in the creation of a vacant niche. If the herbivore community in the plateau is structured primarily by competitive interactions, this is unlikely to have adverse effects on native ungulates. On the other hand, if grazer-facilitation, whereby foraging by one species benefits another by providing access to forage of a suitable height or quality (Vesey-Fitzgerald 1960; McNaughton 1976), is important in structuring the herbivore community, then the creation of a vacant niche can result in a breakdown of facilitatory interactions, which can have effects that cascade through the system. Although previous work has quantified the extent of dietary overlap between domestic and native ungulates in the Mundanthurai plateau (Johnsingh and Sankar 1991), the relative importance of facilitation versus competition between different herbivore species remains unknown.

Both theory (van de Koppel and Prins 1998; Ritchie and Olff 1999) and empirical evidence (Vesey-Fitzgerald 1960; Bell 1970; McNaughton 1976) suggest

that grazer-facilitation can be an important interaction in many grazing ecosystems. The potential for facilitatory interactions between herbivores is likely to be greatest in ecosystems that receive sufficient precipitation and where plants compete primarily for light (Ritchie and Olff 1999), as is potentially the case in the Mundanthurai plateau. In these systems, dominant plants tend to be of low-quality and utilised primarily by large-bodied bulk-feeding herbivores (Ritchie and Olff 1999). Foraging by large-bodied herbivores on these low quality dominants can favour persistence of both high quality plants and smaller-bodied selective herbivores that feed on them. Reductions in numbers of large-bodied herbivores can trigger plant community shifts leading to low-quality plants such as unpalatable tall-grasses dominating the system, causing high-quality plants as well as the smaller-bodied herbivores that feed on them to decline. Because of the high fuel loads that tall-grasses generate, this can also result in a positive grass-fire feedback cycle (D'Antonio and Vitousek 1992), increasing fire frequencies and, in turn, the dominance of fire-tolerant tall grasses, further lowering habitat-suitability for herbivores and eventually leading to lowered herbivore and predator populations in the reserve. While breakdown of facilitatory interactions between herbivores (possibly following reduction in cattle numbers at KMTR following its declaration as a Tiger Reserve in the late 1980s) potentially provides a synthetic explanation for current trends in the reserve, whether or not this is actually the case remains unknown. It is important to note that such trophic cascades are more likely to be manifested in mesic ecosystems such as KMTR, and are unlikely to be a general phenomenon in drier, more arid ecosystems. Although substantiated by theory, evidence for such trophic cascades from terrestrial herbivore assemblages are lacking (but see Lewis 2003 for effects of cattle removal in Keoladeo Ghana National Park, Bharatpur, India). Clearly, more data are needed to test this hypothesis in Mundanthurai.

The experiments reported here provide a context to evaluate the utility of fire as a tool for managing tall-grass savannas in Mundanthurai for herbivores, but caution is nevertheless warranted in extrapolating results from these small-scale studies to larger scales. Whilst the focus of this study was the unpalatable tall-grass species *C. flexuosus*, it is also important to understand how fire interacts with other ecological processes to influence non-target species, as well as community and ecosystem dynamics over larger spatial and temporal scales, before deciding on an appropriate management strategy (Freckleton 2004). For this reason, it is recommended that burning trials, coupled with additional habitat manipulations such as undergrowth clearance in adjacent thorn-scrub woodlands, be initiated over larger scales (1-3 ha) in the Mundanthurai plateau with a view to monitoring plant and herbivore responses. In contrast to other areas of the reserve which are incapable of supporting high ungulate densities because of their hilly terrain (Johnsingh 2001), the plateau contains some of the highest densities and diversity of herbivores in KMTR (which is still low in comparison to other protected areas) and also supports the largest population of *chital* in the reserve (Sankaran 2001a), making it critical from a management viewpoint.

Thus far, the bulk of the management effort at KMTR has been directed toward protection against illegal human activity within reserve boundaries (Dutt 2001). While protection is undoubtedly a critical component of the conservation efforts in the region, it is insufficient as an herbivore and predator management strategy at the current time (Ramakrishnan et al.1999; Dutt 2001). What is needed is a more integrative approach which combines prudent habitat manipulations with appropriate fire and grazing management to augment herbivore habitat quality. Finally, it is critical that such management be coupled with rigorous monitoring of plant and animal populations and ecosystem processes in the reserve, the need for which cannot be overstressed.

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