

Disturbance by overgrazing facilitates bush encroachment by *Tarcananthus camphoratus*

Bernard Coetzee, University of Pretoria, Pretoria, South Africa

Zelalem Wodu, Addis Ababa University, Ethiopia

Lucrezia Tincani, Cambridge University, UK

Abstract

Tarcananthus camphoratus appears to be encroaching into savannah habitats. We addressed whether disturbance facilitates its encroachment. Our results found more *T. camphoratus* recruitment in livestock-grazed areas, indicated by significantly higher mean number of seedlings in comparison to the wildlife-grazed areas. Edaphic factors measured showed no significant trend. Impacts on plant species diversity were also quantified. While significant differences were observed between dense *T. camphoratus* stands and adjacent grassland areas, it is to be expected given the change of habitat structure. The major concern for managers then is not its effects on biodiversity *per se*, but rather the effect of reducing available graze. Furthermore, dense *T. camphoratus* stands did not effect herbivore habitat selection. We discuss life history characteristics of the plant in context of invasion biology theory to predict its encroaching success. The potential for *T. camphoratus* to be a significant savannah encroacher is evident and we suggest that the long-term monitoring of this plant is crucial.

INTRODUCTION

Savannahs are dynamic ecosystems composed of grass and woody plant species. A conspicuous feature of savannah ecosystems is the apparent maintenance of the tree to grass ratio, which is mediated by complex interactions between edaphic factors, rainfall limitation and disturbance regimes such as herbivory and fire. Grasses and woody plants co-exist in a dynamic equilibrium when these edaphic, disturbance and climatic factors interact so as not to exclude either plant form. Consequently, a dynamic shift in any of these factors will change the maintenance of the grass to tree ratio and lead to conversion to one or the other state (Archer *et al.*, 2000).

Where the shift in tree grass ratio is mediated by anthropogenic causes it is termed bush encroachment; the spread of woodland (typically trees and shrubs unpalatable to mammalian herbivores) into previously grassland-dominated areas. Encroachment by woodland into grassland-dominated areas is common in savannahs and reduces grazing carrying capacity (Wiegand *et al.*, 2005). Some savannah landscapes have already been completely encroached by woody species and the process is in progress in other savannah areas affecting wildlife and the sustainability of pastoral, subsistence and commercial livestock grazing (Archer *et al.*, 2000). Bush encroachment is

of great significance since savannahs contain an ever expanding and large proportion of the world's human population. On a global scale, encroachment has the potential to alter carbon and nitrogen sequestration and nutrient cycling significantly (Archer *et al.*, 2000), with potential consequences for climate change.

The proximate causes for woody plant encroachment are still poorly understood, but land use practices, including heavy grazing and anthropogenic reductions in fire regimes, are suspected to facilitate the process. Despite the recognition of woody plant encroachment as a worldwide dryland management problem, little is known about the rates and dynamics of the phenomenon, or its impact on fundamental ecological processes related to energy flow, nutrient cycling and biodiversity (Archer *et al.*, 2000). Encroachment has long been of concern to land managers in grasslands and savannahs, but most research focuses on the effects of woody plants on grass production (Archer *et al.*, 2000), instead of the underlying ecological mechanisms driving encroachment. Therefore our study-addressed factors contributing to the spread of a “suspected encroacher” in Kenya, *Tarchonanthus camphoratus* (Compositae) L., considered a weed by local farmers (Noad & Bernie, 1989). Anecdotal observations suggest that it is systematically encroaching into savannahs areas in Kenya.

T. camphoratus is a small evergreen shrub or tree of up to 9 meters and adapted to a wide variety of habitats throughout sub-Saharan Africa, especially in drier areas (Meg *et al.*, 2002). It is a hardy plant that can regenerate quickly when cut or burnt (Noad & Bernie, 1989).

We tested which factors might contribute to bush encroachment into two different habitats; heavily disturbed and livestock-grazed habitats and more natural habitats that are only occupied by wildlife in the Hell's Gate National Park. We compare recruitment rates in these two contrasting areas; owing to *T. camphoratus* reproducing vegetatively, its hardy characteristics and aggressive resprouting after disturbance such as fire, we predicted that disturbance will facilitate a net recruitment of *T. camphoratus*.

Furthermore, edaphic factors were considered which could influence the encroaching ability of the plant. Changes in soils accompanying long-term heavy grazing may shift the balance in favor of nitrogen fixing or evergreen woody plants which are better adapted than grasses to nutrient poor soils and warmer, drier microenvironments (Archer *et al.*, 2000). The roles of life history characteristics of *T. camphoratus* in determining its ability to encroach grassland-dominated landscapes are also discussed.

As well as investigating the causes, we also addressed the effects of *T. camphoratus* encroachment the impact of encroachment on components of grassland biodiversity is poorly understood. Consequently, plant species diversity and herbivore habitat preferences in heavily encroached areas were measured to quantify possible effects of heavily encroached areas on plant and animal species diversity, distribution patterns and assemblage structure.

METHODS

Study area

The study was carried out at Hell's Gate National Park, Kenya from 19/09/2006 to 22/09/2006 at the end of the short dry season. Five replicates were used within the park, which were considered as wildlife-grazed area and located along the road from Fischer's Tower to Central Tower. For comparison, five replicates were located outside the park boundary where livestock occurs and which by observation was considered heavily grazed and degraded; these sites were located along the Buffalo loop road to Kaparitan village.

Experimental design

Each replicate site contained the edge of a dense stand of *T. camphoratus* within the representative sites; we considered these visually conspicuous distinct edges of *T. camphoratus* as source pools for recruitment of *T. camphoratus* seedlings. This edge was marked and a compass reading taken parallel to the edge which served as a line of reference. Three vegetation plots, each 50m apart, were placed 50m from the edge into the *T. camphoratus* stand. These 2x2m quadrats were used to sample all plant species and their percentage of cover scored using the Braun-Blanquet method, which is an index of abundance (Sutherland, 1996). Two 2x50m transects were placed between these vegetation plots, where dung counts were recorded for all herbivore species in order to compare habitat utilization (Sutherland, 1996) between stands of *T. camphoratus* and adjacent but independent grassland areas. This sampling procedure was repeated in the adjacent grassland areas, 80m from the *T. camphoratus* edge.

In order to quantify the degree of bush encroachment, we measured the *T. camphoratus* seedlings in three 8x100m transects (running from 20m within the *T. camphoratus* edge, orthogonal to the edge, towards the grassland), in 10m increments. Trees less than 1m were considered as seedlings and 3 height classes were used for larger trees (1-2m; 2-3m and >3m). Since *T. camphoratus* can reproduce vegetatively (Noad & Bernie, 1992), trees more than 50cm apart were considered as different individuals; however, we assumed throughout the sampling that sprouting near the base of

a “parent” tree indicated net recruitment, and therefore shoots were considered as separate seedlings.

Soil samples were taken at each of the vegetation plots at a depth of 20cm and placed in sealed plastic containers. Samples were dried for 24 hours to obtain dry weight; subtracting dry weight in micrograms from wet weight from fresh samples indicated water content. pH was measured from a sub-sample of each soil sample at a standard weight in a set concentration with deionised water using an electronic pH meter (Hannah pHep HI 98127).

RESULTS

Recruitment

There was more *T. camphoratus* recruitment on livestock-grazed areas, indicated by the significantly higher mean number of seedlings in comparison to the wildlife-grazed areas (Mann-Whitney $W=1918.0$, $p < 0.0001$). Fig. 1 shows that the mean seedling number decreased with distance from the source pool of *T. camphoratus*. There was a mean of 30 seedlings in the first ten-metre interval from the source pool in the livestock-grazed areas, but this decreased with increasing distance. This gradient in density supported our hypothesis, which predicted unidirectional spread of recruitment from the densest stand. There is no relationship in the wildlife-grazed areas, where seedling number stays uniformly low.

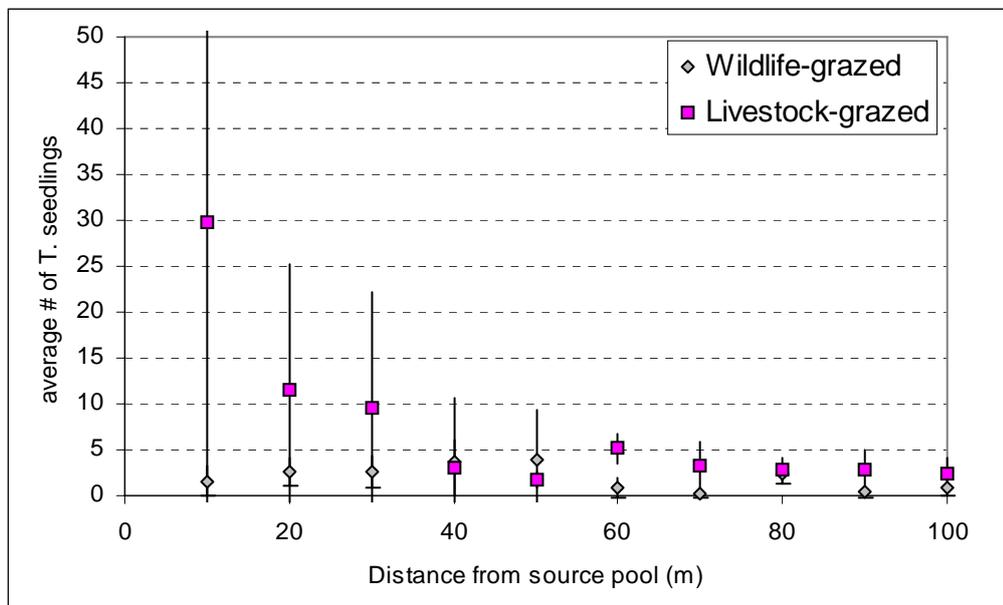


Fig. 1. Mean seedling number of *T. camphoratus* and distance from source pool.

Assuming height class is an indicator of seedling age, we found no difference between seedling heights with distance from the source pool (Fig.2, t-test; $t = -1.61$; $p = 0.11$).

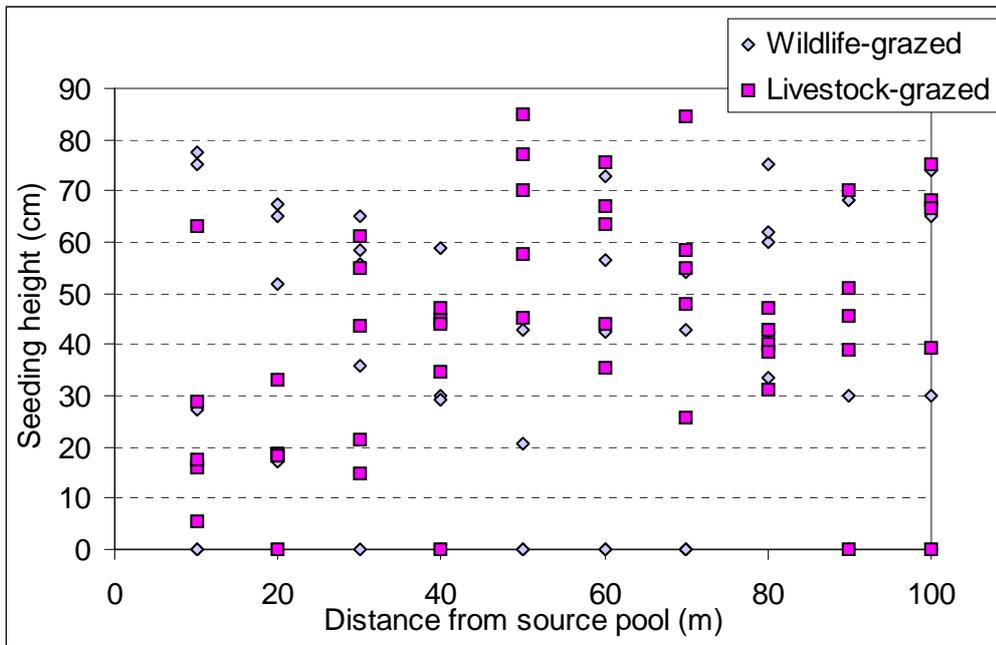


Fig. 2. Mean seedling height of *T. camphoratus* and distance from source pool.

Again assuming height is an indicator of tree age, number of trees in different height classes were not significantly different (paired T-test; $p=0.638$), although an intriguing pattern was evident (**Fig. 3**). The 1-2m and 2-3m height class had greater net recruitment in the livestock-grazed areas, which correspond to the seedling abundance results above. Old and established trees (above 3m) however are more numerous in the wildlife-grazed areas.

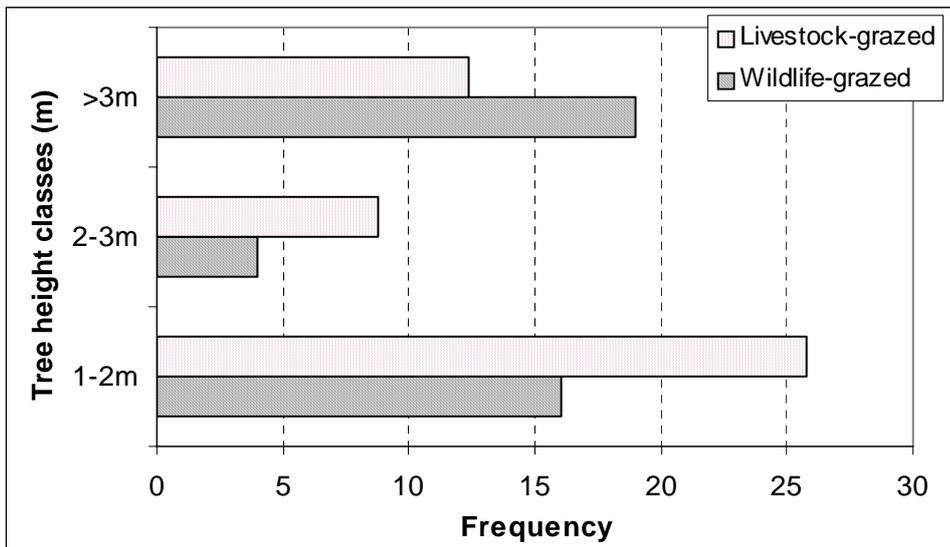


Fig. 3. Number of trees in different height classes from source pool.

Soil samples

Mean soil water content was approximately twice as high in the livestock-grazed grassland, but did not differ significantly (ANOVA $n=15$; $F = 1.52$; $p=0.253$). Similarly, soil pH (overall mean = 6.99 ± 0.23 SD) did not differ significantly between livestock- and wildlife-grazed areas (ANOVA $n=15$, $F=2.02$, $p=0.16$).

Vegetation plots

Total species richness differed significantly between *T. camphoratus* woodland and adjacent grassland areas in livestock-grazed areas (Mann-Whitney, $W= 1470.0$; $p = 0.001$), but not between *T. camphoratus* woodland and adjacent grassland areas in wildlife-grazed areas (Mann-Whitney, $W = 1225.0$; $p = 0.81$). Accordingly, total species abundances differed significantly between *T. camphoratus* woodland and adjacent grassland areas in livestock-grazed areas (Mann-Whitney, $W=1494.5$, $p= 0.0025$), but not between *T. camphoratus* woodland and adjacent grassland areas in wildlife-grazed areas (Mann-Whitney, $W=1303.0$, $p = 0.47$).

Plant assemblage species richness and abundance structure followed similar patterns (i.e. slope of the line) in the two *T. camphoratus* stands, and in the two open grassland areas, respectively (**Fig. 4**). Interestingly, species richness was highest in the *T. camphoratus* stands in the livestock-grazed areas (30 species). However species richness was not very different between the *T. camphoratus* stands (21 species) and the open grassland (22 species) in the wildlife-grazed areas. Grasslands in the livestock-grazed area had lowest species richness (17 species).

In both grazing sites, species were more abundant in the *T. camphoratus* dominated stands. *Cynodon dactylon* dominated both grassland areas, but was much more abundant in the wildlife-grazed areas.

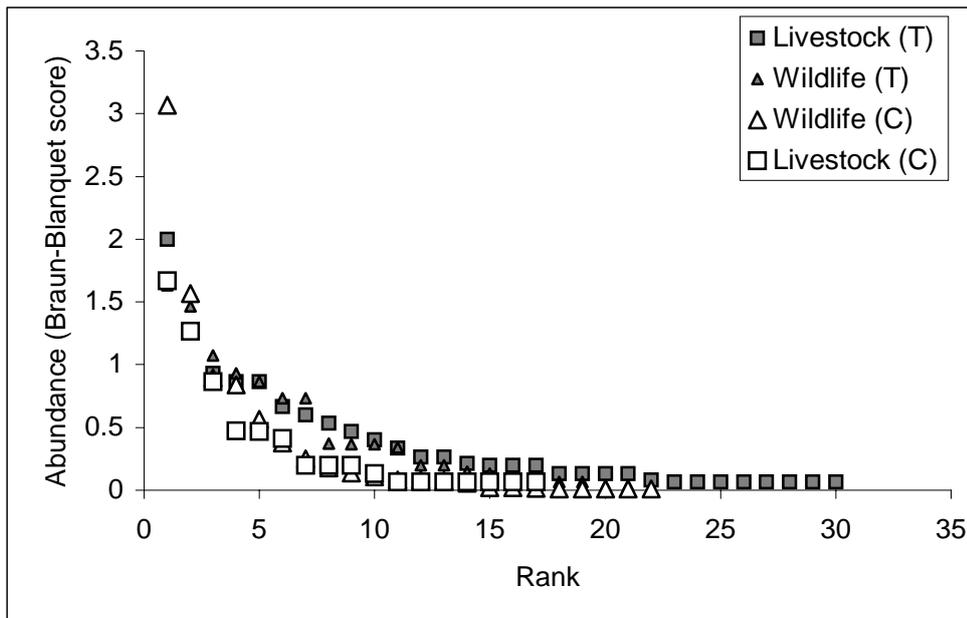


Fig. 4. Rank abundance curve of plant species in Tarchonathus (T) and open grassland (C) areas. The abundance is a Braun-Blanquet score, with 1=1-5% cover, 2=6-35%, 3=26-50% cover, 4=51-75% cover, 5=76-100% cover. The sum of the ranks corresponds to the number of species in each site, i.e. the species richness.

Dung sampling

The total herbivore density was greater in the grasslands in the wildlife-grazed areas, but did not differ significantly from the grasslands in the livestock-grazed site (**Fig. 5**, 1-way T test, $T=???$, $p=0.055$).

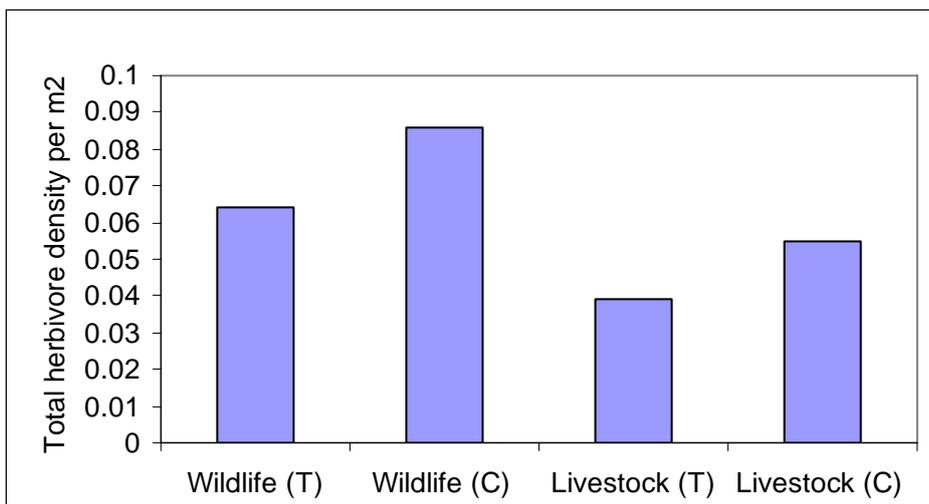


Fig. 5. Total herbivore density in wildlife-grazed and livestock-grazed areas

Comparison between sites within each herbivore species showed no significant trend in density (**Fig. 6**, paired T test, $p= 0.69$). Species composition was distinctly different between the two sites;

dung density confirmed that livestock predominantly grazed in our “livestock-grazed” sites, and that wildlife exclusively grazed in our “wildlife-grazed” sites.

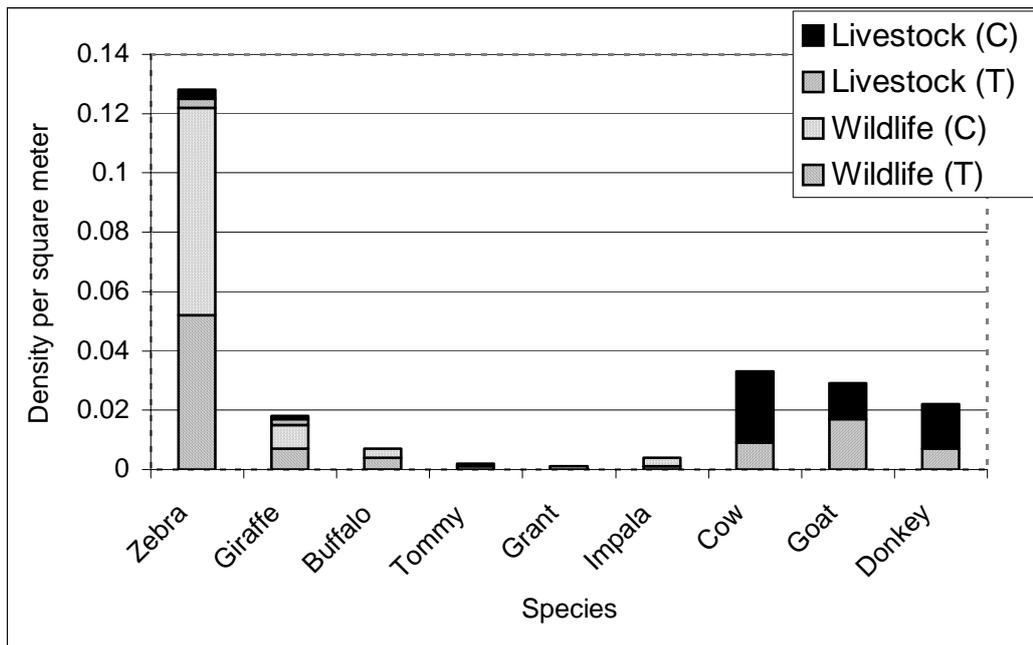


Fig. 6. Density of each herbivore species in wildlife-grazed and livestock-grazed areas

DISCUSSION

We showed that anthropogenic disturbance facilitates encroachment of *T. camphoratus* in and around Hell’s Gate National Park. This was demonstrated by the higher seedling number and higher number of short trees (1-2m and 2-3m) in the heavily disturbed livestock-grazed area. This area was in the vicinity of a Maasai village, Kaparitan, and subject to high levels of human disturbance (roads, trampling, firewood collection etc), as well as by livestock. Net recruitment from a parent source pool was to be expected, but our results indicate that this affect is more apparent in areas disturbed by overgrazing.

The height distribution of the seedlings did not show any relationship with distance from the source pool (Fig. 2). This could suggest that vegetative spread (which is directional) is not the main mechanism of dispersal, but that the soil seed bank instead plays a larger role. However, it is known that soil seed banks often are destroyed by disturbance regimes in savannah ecosystems (Kaller, 2003). Whether it is the soil seed bank or vegetative reproduction that is the major contributor to the spread of this plant remains to be tested.

Drivers of encroachment

Disturbance is a well-known facilitator of bush encroachment (Myers & Bazely, 2003), which was supported by our results. Previous studies suggest that plant establishment, which is influenced by

disturbance levels, is the limiting factor in bush encroachment, as opposed to dispersal (Myers & Bazely, 2003). The importance of disturbance in facilitating bush encroachment is analogous to its role in facilitating the spread of invasives by promoting colonisation and establishment opportunities (di Castri, 1989). A study comparing the role of different types of disturbance concluded that human-induced disturbance determined 97% of the spread of exotics (Lozon & MacIsaac, 1997).

Edaphic factors did not play a role in our study. Although known to affect the distribution of woodlands in savannah ecosystems (Archer *et al.*, 2002), the small scale of our study might not have picked up significant differences in soil moisture content or pH. We were also limited by the equipment available. The plant does not seem to either influence or be facilitated by very local scale changes in water content or pH.

High grazing pressure is also known to facilitate bush encroachment because it opens sites for colonisation, allowing net recruitment into the grassland. Herbivory allows the spread of less palatable species by selectively removing the more palatable ones, thus reducing interplant competition. The higher plant survival of the less palatable species makes them well-suited for further encroachment. Palatability is likely to be important in this study because *T. camphoratus* contains high quantities of the anti-herbivory compound camphor (Pelgrave *et al.*, 2002). Our dung density results were not sufficient to quantify the degree of grazing pressure, since the presence of herbivore does not necessarily mean it was grazing, but could have been utilising the site for shade or protection from predators etc. Damage by herbivores was observed, but not measured quantitatively. Herbivores do appear to browse the plant, especially in the dry season (van Essen *et al.* 2002, Pelgrave *et al.*, 2002). Further studies could measure mean sward height to estimate grazing extent, as well as carrying out observational studies on the herbivores.

From the factors we measured, we could not determine which was most important in explaining the variation in *T. camphoratus* encroachment. Other extrinsic factors which we did not measure may also be playing a role in the rate of bush encroachment, such as climate change, historic atmospheric CO₂ enrichment and exotic species introductions (Archer *et al.*, 2002). Current trends in atmospheric CO₂ enrichment may exacerbate shifts from grass to woody plant domination, especially where the invasive trees/shrubs are capable of symbiotic N-fixation. Expansion of woody plants into grasslands may also be favored by recent increases in atmospheric N-deposition.

Local effects of encroachment

Our results did not show a clear effect on the plant species assemblages by *T. camphoratus*. Species abundances and richness were higher under the *T. camphoratus* stand in both sites. The fact that there is a change in plant assemblage is not necessarily caused by *T. camphoratus* encroachment; it might simply be the change habitat structure. A closed forest canopy gives shade, resulting in higher plant available moisture (as our results showed), and may contain more soil nutrients due to leaf litter addition. The degree of trampling and grazing may be lower within a forest due to physical barriers to the grazing animals. We could not causally link the differences in plant species abundances to the presence or absence of *T. camphoratus*. Anthropogenic disturbance regimes additionally confound observed patterns, and may actually be the major driver of changes in the different habitats. From a management point of view then, it is not a change in species diversity that is of concern, but rather that the abundance of the dominant grass species is reduced as the species encroaches.

Similarly, herbivore habitat selection did not show a significant trend between the *T. camphoratus* stand and the control sites. Their distribution could be affected by numerous factors, including food availability, shade, camouflage from predator, and vigilance of predators, which we did not differentiate between. Mean total herbivore density was higher in the control grassland in both sites, but this could be because the majority of the observed species were grazers, and not browsers, and thus selected the site with more fodder, as well as the site with increased vigilance from predators. However we observed the majority of the grass to be dry & dead and thus do not suspect fodder availability to be the main determinant of habitat selection. Our results may have been very different during the wet season, when there is plentiful food available to grazers and are thus not necessarily representative of habitat utilisation year round. Also, it is known that wildlife tend to congregate in parks during the dry season, but disperse into surrounding pastoral areas during the wet season (Boone, 2005) so we could have measured an even higher density of livestock and wildlife in the range lands surrounding the Hell's Gate National park during the wet season. This superior grazing pressure may further enhance bush encroachment.

Species biology of the encroacher

Understanding what makes a particular species a better invasive competitor is a major challenge in ecology (Kolar & Lodge, 2001). While mostly applicable to predations in invasion biology, *T. camphoratus* has similar life history characteristics to successful alien invasive species for a comparison to invasive alien plants and to help describe factors which may make it a successful woodland encroacher.

Identifying species traits contributing to invasive success is difficult, so much so that some ecologists remain pessimistic that general rules identifying potential invaders will be impossible (Williamson, 1999). However, a recent review by Kolar & Lodge (2001) maintains that certain generalizations can be made. Intuitively, and which has been confirmed empirically, vegetative reproduction contributes majorly to the reproductive success of an invading alien plant and is a pattern that has emerged for a variety of species (Kolar & Lodge, 2001). Furthermore, seed size and dispersal mechanisms are also contributors to invasive species success (Rejmánek & Richardson, 1996; Kolar & Lodge, 2001). Indeed, invasion of woody species in disturbed landscapes has been shown to be significantly associated with seed size (Rejmánek, 1996).

T. camphoratus has two of the major life history characteristics which have been shown to contribute to invasive success; it reproduces vegetatively and has small wind dispersed seeds (Noad & Bernie, 1989; Pelgrave *et al.*, 2002). It is clear that this plant has the potential to be a significant bush encroacher, particularly in disturbed habitats.

It is important to note however that alien invasive plant species can either be the drivers or passengers of ecological change and this model can be effectively applied to bush encroachers. As we showed, plant species can have the life history characteristics to make them aggressive invaders of their respective habitats (the driver model). Conversely either anthropogenic or natural ecological processes like disturbance may merely facilitate their invasion by fire and increasing global climatic change, as well as rising atmospheric CO₂ and N deposition rates, or facilitation natural ecological processes like disturbance by fire or facilitation by other plant species (the passenger model). Often the two models work in synergy to both contribute to the invasive, or for our purposes encroaching, success of a particular species (Didham *et al.*, 2005). Although we did not perform the explicit experimental manipulation necessary to distinguish between the two models (Didham *et al.*, 2005), our theoretical framework and empirical evidence showed that *T. camphoratus* has the life history characteristics and is facilitated by disturbance, particularly of overgrazing, to synergistically increase its possible encroaching success. A complete understanding of these synergistic effects has important consequences for management of the plant. For example, simple mechanical removal of the plant may not rehabilitate areas if the disturbance effects (in this case disturbance by overgrazing) is not controlled as well. Predictions from our results for management do however remain speculative.

In sum, our study did show that *T. camphoratus* has the potential to be a significant encroacher in especially disturbed savannah habitats. The major caveat in our study is that we did not have remote sensing data over large temporal scales which would be the most adequate and explicit quantification of savannah encroachment. We suggest the long-term monitoring of this plant is paramount, with the caveat that it remains to be seen whether it poses a significant threat as a bush encroacher, but that the potential certainly is there.

If this potential is realised, the pastoral tribes are likely to be significantly affected. In Kenya, a major proportion of people are dependent on subsistence livestock farming in savannah ecosystems for their very survival. Bush encroachment by *T. camphoratus*, perversely facilitated by the farmers themselves, has the potential to reduce grazing carrying capacity, with dire consequence for both the wildlife and pastoralist dependent on this habitat.

ACKNOWLEDGEMENTS

We thank the entire TBA team for their relentless enthusiasm. Clive Nuttman, Anthony Kuria, Daniel Nkalubo and Shem Mwasi helped tremendously with this project. We thank the buffalo for leaving us alone, the kitchen staff for their amazing packed lunches, and the *Tarchonathus* trees for providing us with soothing shade during our siestas. Weird amazing no! yes! Are we wining? Hell yeah.

REFERENCES

- Archer, S., Boutton, T.W., Hibbard, K.A. (2002). Trees in Grasslands: Biogeochemical Consequences of Woody Plant Expansion. In: *Global Biogeochemical Cycles in the Climate System* (E-D Schulze, SP Harrison, M Heimann, EA Holland, J Lloyd, IC Prentice, D Schimel, eds.). Academic Press, San Diego (In Press for 2000).
- Boone, R.B. (2005) Quantifying Changes in Vegetation in Shrinking Grazing Areas in Africa. *Conservation and Society*, **3(1)**: 150 – 173.
- di Castri, F (1989) History of biological invasions. In *Biological Invasions: A Global Perspective*. Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Jeianek, M., Williamson, M. (eds). Chichester, UK. John Wiley & Sons.
- Didham R.K. *et al* (2005). Are invasive species the drivers of ecological change? *T.R.E.E.* **20(9)**: 470-474.
- van Essen, L.D., Bothma, J., van Rooyen, N., Trollope, W.S.W. (2002) Assessment of the woody vegetation of Ol Choro Oiroua, Masai Mara, Kenya. *Afr. J. Ecol.* **40**: 76-83.
- Kaller A. (2003). Growth pattern and reproduction of woody vegetation in a semi-arid savanna in southern Botswana. *Masters Thesis, Uppsala University, Sweden.*
- Kolar & Lodge (2001). Progress in invasion biology: predicting invaders. *T.R.E.E.* **16 (9)**
- Lozon, J.D. and MacIsaac, H.J. (1997) Biological invasions, are the dependent on disturbance? *Environmental Review* **5**:131-141.

- Myers, J.H. & Bazely, D.R. (2003) *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge.
- Noad, T.C. & Bernie, A. (1989) *Trees of Kenya*. Noad & Bernie coop, Kenya.
- Palgrave, M.C. *et al.* (2002) *Trees of South Africa*. Struik Publishers, Cape Town.
- Rejmánek M. & Richardson D.M. (1996) What attributes make some plants species more invasive? *Ecology* **77(6)**: 1655.
- Rejmánek M. (1996). A theory of seed plant invasiveness: The first sketch. *Biological Conservation* **78**:171- 181.
- Wiegand K. Saltz, D., Ward D. (2006) A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics* **7**:229–242.
- Williamson, M. (1996) *Biological Invasions*, Chapman & Hall.