

Fire and grazers in the West African savanna Klop, L.F.

Citation

Klop, L. F. (2009, September 3). *Fire and grazers in the West African savanna*. Retrieved from https://hdl.handle.net/1887/13947

Version:	Not Applicable (or Unknown)		
License:	<u>Licence agreement concerning inclusion of doctoral</u> <u>thesis in the Institutional Repository of the University</u> <u>of Leiden</u>		
Downloaded from:	https://hdl.handle.net/1887/13947		

Note: To cite this publication please use the final published version (if applicable).

Chapter 8

Discussion

8.1 INTRODUCTION

Africa is often called 'the fire continent' based on the high frequency and large extent of burning. As outlined in the Introduction, over 200 million hectares of land are regularly burned, most of which consist of savanna areas. The significance of fire for the structure and functioning of savanna ecosystems can hardly be overstated, as fires affect nutrient cycling and soil organic matter content (e.g., Fynn *et al.* 2003, González-Pérez *et al.* 2004), the cover of trees versus grasses (Scholes & Archer 1997, Sankaran *et al.* 2005, 2008), and the quality and structure of the grass sward (Van de Vijver *et al.* 1999). Regular burning also has significant ecological effects on the herbivores living in savanna ecosystems. In this thesis the ecological effects of fire on savanna herbivores are described, in particular the nutritional quality and structure of post-fire regrowth as a food source for herbivores, resource selection patterns on post-fire regrowth, the partitioning of resources among potential competitors, and species diversity patterns and assemblage structure of savanna ungulates. In this chapter a discussion of the main results and conclusions is given.

8.2 FIRE, FORAGE AND RESOURCE SELECTION

Savanna fires significantly affect the quality and structure of the grass layer. Previous research has shown that concentrations of some macronutrients such as nitrogen, phosphorus and potassium in post-fire regrowth are generally higher than in unburned vegetation (Christensen 1977, Frost and Robertson 1987, Hobbs *et al.* 1991, Singh 1993, Van de Vijver *et al.* 1999, Laclau *et al.* 2002). Nutrient levels have been shown to decline rapidly, however, falling back to the levels of unburned vegetation in weeks or months (Van de Vijver *et al.* 1999).

As outlined in Chapter 3, the main importance of burning to herbivore forage quality lies in the dry season levels of leaf tissue nitrogen, the digestibility of the plant material and the structure of the grass sward. Ruminants need a minimum of 5–7% crude protein in their food to support rumen fermentation (Van Soest 1982, McDowell 1985, Prins 1996) which corresponds with nitrogen concentrations of 0.8–1.1%. In the dry season these requirements were met only in post-fire regrowth, whereas nitrogen concentrations in unburned swards were below maintenance levels. Likewise, during the dry season digestibility values of around 60% that are required by lactating animals

(Van Soest 1982) were found only in burned swards. Burning also significantly improved sward structure, as burned swards were characterised by higher values of green leaf bulk density and less dead stem material in the sward. These dead stems in the sward are known to depress intake rates of grazers (Drescher 2003). Burning appeared not to be of much importance for the minimum requirements of potassium, calcium and magnesium. Although potassium levels in the grass sward were significantly affected by burning, potassium levels in both burned and unburned swards were above the minimum herbivore requirements. Calcium and magnesium concentrations were not affected by burning.

The raised nutrient levels, higher digestibility and more favourable structure of the burned grass sward has major effects on the foraging patterns of herbivores. Numerous studies have shown that herbivores prefer grazing on post-fire regrowth compared to unburned grass swards (e.g., Moe *et al.* 1990, Wilsey 1996, Moe & Wegge 1997, Gureja & Owen-Smith 2002, Tomor & Owen-Smith 2002, Archibald & Bond 2004, Archibald *et al.* 2004, Anderson *et al.* 2007, Hassan *et al.* 2007). Within burned areas, the spatial distribution of grazing was governed mainly by local differences in regrowth age, the amount of dead stem material in the sward, grass cover, and the distance to water

Table 1. Selection on burned areas for the four most important habitat variables. Double signs (+ + or)
indicate significant positive or negative selection at $P < 0.01$, whereas single signs indicate significant selection
at P < 0.05.

	Regrowth age	Grass cover	Dead stems	Distance to water
Red-flanked duiker				
Oribi				
Common duiker		++		
Bohor reedbuck		++		
Bushbuck	-			
Warthog				+
Kob		++		
Hartebeest		++		++
Roan			-	++

sources (Chapter 4, Table 1). The results summarized in Table 1 demonstrate that resource selection by herbivores on post-fire regrowth is not uniform, which was suggested by Archibald and Bond (2004). Most importantly, the resource selection by seven out of nine species of herbivores was related to regrowth age, as most herbivore species strongly selected grass swards that were recently burned. This selection for young regrowth correlated significantly with concentrations of nitrogen (N) and potassium (K) in the green leaves, indicating that herbivores select patches of regrowth containing high nutrient levels. It should be noted that shortly after burning, the quality of the regrowth is high but the biomass very low. Herbivores thus face a trade-off between forage quality and quantity, and it is expected that maximum profitability will be reached some time after burning when nutrient levels are still high and the grass biomass will allow for sufficient intake rates.

Besides nutrient levels, herbivore resource selection is also significantly affected by sward structure. Post-fire regrowth has higher green leaf fractions and green leaf bulk density than unburned vegetation (Chapter 3). In addition, burning reduces the amount of dead stems in the sward, thereby increasing access and making the green leaf biomass more accessible to herbivores (Drescher 2003). Because of the more favourable sward structure, foraging efficiency is increased and grazing herbivores are able to reach higher intake rates on post-fire regrowth compared to unburned areas (Hobbs *et al.* 1991, Drescher 2003, Moe & Wegge 1997). The positive effects of burning on sward structure were clearly seen in patterns of resource selection of grazing herbivores (Chapter 4: Table 3), as oribi, kob and roan were found to significantly avoid grass swards with high amounts of dead stem material. Besides the amount of dead stems in the sward, grass cover was among the principal factors governing resource selection. For example, an increase in grass cover by only one percent increased the probability of use by about 7% for kob, and even 15% for bohor reedbuck.

8.3 BODY MASS, RESOURCE PARTITIONING AND COMMUNITY STRUCTURE

The idea that differentiation in body size can govern community structure dates back to Hutchinson (1959). In his seminal paper *Homage to Santa Rosalia*, Hutchinson (1959) presented body size ratios of several pairs of sympatric bird and mammal species, and the mean ratio of about 1.3 was suggested to be the amount of separation necessary to permit coexistence of species at the same trophic level. These ideas were further

developed by MacArthur & Levins (1967) into a model of limiting similarity, which predicts a reduction in niche overlap of competitors through ecological assortment of colonization and extinction (Schoener 1974, Gotelli & Graves 1996). The importance of body mass to resource partitioning by herbivores was shown by Demment and Van Soest (1985), who argued that body size provides a mechanism by which herbivores can differentiate along a resource axis of grasses having different fibre contents. Since the ratio of metabolic requirements to food processing capacity decreases with increasing size, various authors have argued that smaller-sized herbivores need higher quality food than larger herbivores (e.g. Bell 1971, Jarman 1974, Demment 1982, Van Soest 1982, Demment and Van Soest 1985, Prins & Olff 1998, Codron *et al.* 2007).

Based on the analysis of faecal samples, the data presented in Chapter 5 do not support the theory that smaller herbivores select forage of higher quality than do larger herbivores. In addition, there was no relation between body mass and food composition (i.e., the selected food plants in the diet) either. These results indicate that in Bénoué N.P. herbivore species of different size do not segregate in food quality or the range of food plants that are consumed. This is also supported by the data on resource selection shown in Chapter 4, since there was no effect of body mass on the selection of post-fire regrowth. Although in sharp contrast to the often-cited Jarman-Bell principle, the results from Bénoué lend support to some recent studies that questioned the relation between body mass and digestive efficiency (Perez-Barberia et al. 2004, Clauss et al. 2007). These authors argued that the digestive physiology of a particular species and the proportion of grass versus browse in its diet may be more important than body mass in governing food quality or fibre digestion. The importance of digestive physiology is also clearly shown in Chapter 5, where inclusion of hippopotamus (a non-ruminating foregut fermenter) in the dataset resulted in an apparent negative relationship between body mass and nitrogen and phosphorus in the faeces. However, this relationship most likely reflects low losses of bacterial protein in hippo faeces rather than a general body mass diet quality relationship.

Although herbivores in Bénoué do not appear to segregate in food quality or diet composition along a body mass axis, two out of three null models indicated a significant regularity in the body mass distribution (Chapter 6). Such regularities in body mass distribution at the local scale are usually interpreted as the result of competition (Gotelli & Graves 1996, Prins & Olff 1998, Allen *et al.* 2006). The potential for competition is clear from the data on diet composition presented in Chapter 5, which show very high

dietary overlap between several species of herbivores in Bénoué N.P. The importance of competition in shaping ungulate assemblages is widely claimed (Arsenault & Owen-Smith 2002), and several studies have demonstrated competitive interactions among sympatric ungulates (e.g., Gordon and Illius 1989, Murray and Illius 1996, Putman 1996). However, the presence of competition between herbivores in Bénoué N.P. is seriously challenged by other results presented in this thesis. De Boer and Prins (1990) identified three conditions for the occurrence of competition: 1) the resources must be shared, 2) the shared resources are limited, and 3) species show overlap in habitat use. Although the diets of kob, hartebeest, waterbuck, roan, buffalo and hippopotamus were found to be extremely similar both in the dry and wet season (Chapter 5), Chapter 4 demonstrates that herbivore species in Bénoué N.P. differ in patterns of habitat use and spatial distribution in the burned landscape during the dry season. Thus even when diets are similar, differential habitat use may preclude competition. This contrast highlights the importance of scale: at the scale of the entire park, the regularity in body mass distribution suggests that the overall species set may be shaped by biotic interactions. However, at finer spatial scales competition is probably absent or low, allowing high dietary overlap (in both quality and composition) among different herbivore species.

8.4 FIRE AND HERBIVORE DIVERSITY

Fires can affect diversity patterns of ungulates at both local and regional scales. At the local scale, herbivores were not randomly distributed over burned and unburned areas (Chapter 6). Burned areas supported higher species density of ungulates than unburned areas, although species richness was not different. In addition, grazers reached higher species richness and species density than browsers on burned areas. The effects of fire on regional diversity patterns are even more prominent, as shown in Chapter 7. Previous studies have argued that diversity patterns of large mammalian herbivores are governed by gradients of plant abundance and quality (Olff *et al.* 2002), which in turn depend on moisture and nutrient availability (Breman & De Wit 1983). However, the results described in Chapter 7 show that moisture and nutrients alone fail to adequately predict species richness of grazers in West Africa. The widespread fires that are characteristic of the African savannas appear to be more important, as these fires override the effects of climate and soil fertility on the quality and structure of the grass sward. As shown in Fig.

1, fire occurrence is by far the most important factor explaining the assemblage composition (beta diversity) of grazers.



Fig. 1. Percentages of the species composition of West African ungulate assemblages explained by fire, actual evapotranspiration (AET) and soil nitrogen.

A close relation exists between fire occurrence and diversity patterns of West African ungulates, expressed either as species richness or as differences in assemblage composition. Grazers attain maximum species richness at actual evapotranspiration (AET) values of 700–800 mm, i.e., in the northern Guinea savanna zone. However, as described in Chapter 3, in these areas the dry season grass quality is generally below herbivore maintenance levels. The very reason that grazing herbivores survive the dry season in the Guinea savanna is thus likely to be fire.

8.5 FIRE MANAGEMENT

Fire management is of direct relevance to the management and conservation of wildlife. As argued in this thesis, fires can sustain grazer populations during the dry season by providing nutritious post-fire regrowth, and the current species richness of ungulates in the nutrient-poor savannas of West Africa can probably not be maintained without fire.

The ecological effects of fire depend to a large extent on the burning regime, which refers to the type of fire (e.g., surface vs. crown fires), the fire frequency, seasonality, fire intensity, and fire severity or ecosystem impact (Bond & Keeley 2005). Van Wilgen et al. (2003) discussed the pros and cons of five different fire management policies that have been used in Kruger N.P., South Africa. First, a formal fire regime in which fixed management areas are burned every three years was used for several decades, but was finally abandoned because of rigidity and a lack of variation. In the 1990s a lightning fire regime was adopted in order to simulate the natural conditions under which Kruger's biota evolved. Since this resulted in too small a fraction of the area being burned regularly, other fire regimes were developed such as patch mosaic burning (Brockett et al. 2001) and range condition burning (Trollope 1995). Patch mosaic burning refers to a fire regime that is variable in space and time in order to develop a heterogeneous vegetation structure and to create high levels of biodiversity (Brockett et al. 2001, Van Wilgen et al. 2003; but see Parr & Andersen 2006), whereas range condition burning refers to a fire regime aimed at developing the desired composition and structure of the vegetation (Trollope 1995, Van Wilgen et al. 2003). In 2002 an integrated approach was adopted that combined elements of patch mosaic, range condition and lightning fires. In this approach random point ignitions are combined with unplanned fires until a target area that is burned is reached, after which only lightning fires are allowed to spread (Van Wilgen et al. 2003).

In contrast to southern Africa, not much research on fire management has been done in West Africa. Most management fires in Bénoué N.P. are lit in December and January, with sporadic burning activity afterwards. Based on data on regrowth quality (Chapter 3) and herbivore resource selection (Chapter 4), a longer fire season is recommended in which burning activity is spread out more evenly over the dry season. After the wet season, burning can start as soon as the vegetation is sufficiently dry to allow fires to spread. In order to ensure the availability of high-quality grass swards throughout the dry season, burning should continue deeper into the dry season. As shown in Chapter 3, mid-dry season burning resulted in higher concentrations of nitrogen and potassium and higher digestibility of the grass sward than early burned swards. However, for safety reasons mid-dry season burning should be restricted to areas that are easily controlled such as unburned areas surrounded by vegetation that has been burned earlier. Late dry season fires are not recommended, as high fire intensities late in the dry season substantially increase the risk of fires getting out of control. In addition, except for the removal of dead stems from the grass sward, burning late in the dry season has little value in providing nutritious forage for herbivores since the effects of burning are overridden by the effects of the first rains (Chapter 3).

Burning seasonality affects the intensity of the fire, which in turn is governed by fuel load, moisture content of the grasses, temperature and wind speed (Trollope 1999, Govender *et al.* 2006). Fire intensity can thus also be manipulated by burning in different weather conditions or at particular times of the day, with mid-day fires usually being more intense than early morning fires. High-intensity fires remove more grass biomass than low-intensity fires, leading to post-fire regrowth with low amounts of dead stem material remaining. As shown in Chapter 4, such swards are highly preferred by grazing herbivores. It should be noted that removal of the moribund grass material can be achieved by relatively low intensity fires of less than 1000 kJ s⁻¹ m⁻¹, whereas truly high intensity fires (>2000 kJ s⁻¹ m⁻¹) are required to cause significant tree and shrub mortality (Trollope 1999).

The preference of post-fire regrowth by grazing herbivores can lead to very high grazing pressure in burned areas, as shown in Chapter 6. Heavy grazing can result in the dominance of pioneer or unpalatable perennial grass species (Trollope 1999, Van Wilgen *et al.* 2003), and in livestock systems rotational grazing schemes are often employed to avoid a deterioration in grass species composition (Tainton 1999). Post-fire grazing in wildlife areas is more difficult to control, and where possible the burned areas should be sufficiently large to exceed the forage requirements of grazing herbivores (Trollope 1999). Even without the effects of grazing, however, regular burning can affect the plant community by promoting fire-tolerant species (Frost & Robertson 1987, Gibson & Hurlbert 1987, Hartnett *et al.* 1996).

An important issue to consider in fire management is the sustainability of burning practice. Various authors have expressed concern that frequent burning can lead to long-term decreases in nitrogen budgets (e.g. Ojima *et al.* 1994, Blair 1997, Fynn *et al.* 2003). In turn, nitrogen limitation may affect vegetation composition and ecosystem functioning (Scholes 1990). However, the results from burning experiments in savanna ecosystems are variable and often inconsistent. In contrast to abovementioned studies, recent data from a long-term burning experiment in Kruger N.P. by Coetsee *et al.*

151

(2008) show that nitrogen mineralization rates were not affected by 50 years of burning. Losses of nitrogen from savanna burning are often compensated for by deposition and fixation (Menaut *et al.* 1993, Jensen *et al.* 2001), and grazers can contribute substantially to nitrogen conservation by moving nitrogen from the above-ground plant biomass to below-ground pools via urinary and faecal excretion (Hobbs *et al.* 1991, Coetsee *et al.* 2008). The effects of burning on nitrogen availability depends on many factors such as fire intensity, grass species composition, grass:tree ratios (and hence, litter quality), and post-fire grazing. Since fire intensity can be easily manipulated by fire managers by burning in different weather conditions or at particular times of the day, any long-term effects will be highly dependent on current burning practice. This thesis shows the importance of savanna fires to sustaining wildlife populations in the moist savannas of West Africa. Further research is needed to study the contribution of fire to the management and conservation of the Guinea savanna in the long term.

8.6 CONCLUSIONS

The following conclusions can be drawn from this research:

- 1. In contrast to unburned vegetation, post-fire regrowth provides sufficient food quality for grazing herbivores during the dry season. Thus, in the Guinea savanna zone of West Africa, fire enables grazers to survive the dry season.
- 2. The improved nutrient levels, digestibility and sward structure in post-fire regrowth are highest after burning in the middle of the dry season.
- 3. The time elapsed since burning is the dominant factor in the selection of grass swards by herbivores, which can be explained by the short duration of nutrient enhancement after burning. In addition, the improvement of sward structure, especially grass cover and the presence of dead stems, plays an important role in herbivore resource selection.

- 4. In contrast to previous research, resource partitioning among different species of herbivores in Bénoué N.P. is independent of body mass. Thus, small herbivore species do not select food with higher nutrient levels than do large species.
- 5. In spite of the regular spacing in body masses of herbivore species at the scale of Bénoué as a whole, suggesting competition between the different species, at the local scale of burned areas no competition between species could be observed. This may be due to species-specific habitat selection and reduced food competition by fire.
- 6. When looking at all herbivore species, burned areas attract higher numbers of animals than unburned areas, but there is no difference in species richness. When looking at different guilds, grazers are more dominant than browsers in burned areas, both in numbers and species richness.
- 7. For grazing herbivores, regional diversity patterns in West Africa are governed mostly by fire. In contrast, for browsing herbivores regional diversity patterns are not governed by fire but by moisture availability. This difference is most likely due to the fact that fire sustains grazers during the dry season, whereas the food supply for browsers is mainly governed by moisture.
- 8. Burning in the Guinea savanna results in a fire climax with a distinct and high herbivore species richness, which is different from both the herbivore assemblage in the Sudan savanna and the tropical forest zone.
- The present regime of early burning does insufficiently take into account that maximal nutrient enhancement occurs when burning in the middle of the dry season.
- 10. Apart from this seasonality aspect, also other factors are important for the fire management, in particular the short period during which nutrient

enhancement occurs, protection against fire damage, stimulation of tourism, and the desired vegetation type.

Recommendations:

- 1. In order to maintain current levels of herbivore species richness in the Guinea savanna, and overall levels of herbivore beta diversity in West Africa, it would be unwise to stop burning practice.
- 2. Burning activity should be spread out over the first half of the dry season to provide sufficient food quality for herbivores throughout the dry season, taking into account fire hazard, tourism, and the vegetation that is desired.

REFERENCES

- Allen, C.R., Garmestani, A.S., Havlicek, T.D., Marquet, P.A., Peterson, G.D., Restrepo, C., Stow, C.A. and Weeks, B.E. (2006). Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters* 9: 630-643.
- Archibald, S. and Bond, W. J. (2004). Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire* 13: 377-385.
- Archibald, S., Bond, W.J., Stock, W.D. and Fairbanks, D.H.K. (2004). Shaping the landscape: firegrazer interactions in an African savanna. *Ecological Applications* 15: 96-109.
- Arsenault, R. and Owen-Smith, N. (2002). Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97: 313-318.
- Bell, R.H.V. (1971). A grazing ecosystem in the Serengeti. Scientific American 225: 86-93.
- Blair, J.M. (1997). Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology* 78: 2359-2368.

- Bond, W.J. and Keeley, J.E. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20: 387-394.
- Breman, H. and De Wit, C.T. (1983). Rangeland productivity and exploitation in the Sahel. *Science* 221: 1341-1347.
- Brockett, B.H., Biggs, H.C. and Van Wilgen, B.W. (2001). A patch mosaic burning system for conservation areas in southern Africa. *International Journal of Wildland Fire* 10: 169-183.
- Christensen, N.L. (1977). Fire and soil-plant nutrient relations in a pine-wiregrass on the coastal plain of North Carolina. *Oecologia* 31: 27-44.
- Clauss, M., Schwarm, A., Ortmann, S., Streich, W.J. and Hummel, J. (2007). A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. *Comparative Biochemistry and Physiology Part A* 148: 249-265.
- Codron, D., Lee-Thorp, J.A., Sponheimer, M., Codron, J., de Ruiter, D. and Brink, J.S. (2007). Significance of diet type and diet quality for ecological diversity of African ungulates. *Journal of Animal Ecology* 76: 526-537.
- Coetsee, C., February, E.C. and Bond, W.J. (2008). Nitrogen availability is not affected by frequent fire in a South African savanna. *Journal of Tropical Ecology* 24: 647-654.
- De Boer, W.F. and Prins, H.H.T. (1990). Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82: 264-274.
- Demment, M.W. (1982). The scaling of ruminoreticulum size with body weight in East African ungulates. *African Journal of Ecology* 20: 43-47.
- Demment, M.W. and Van Soest, P.J. (1985). A nutritional explanation for body size patterns of ruminant and non-ruminant herbivores. *American Naturalist* 125: 641-672.
- Drescher, M. (2003). *Grasping complex matter: large herbivore foraging in patches of heterogeneous resources*. PhD thesis, Wageningen University, Wageningen.
- Frost, P.G.H. and Robertson, F. (1987). The ecological effects of fire in savannahs. In: Walker, B.H. (ed.) *Determinants of tropical savannahs*. IRL press, Oxford, pp 93-140.
- Fynn, R.W.S., Haynes, R.J. and O'Connor, T.G. (2003). Burning causes long-term changes in soil organic matter content of a South African grassland. Soil Biology and Biochemistry 35: 677-687.

- Gibson, D.J. and Hurlbert, L.C. (1987). Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72: 175-185.
- González-Pérez, J.A., González-Vila, F.J., Almendros, G. and Knicker, H. (2004). The effect of fire on soil organic matter a review. *Environment International* 30: 855-870.
- Gordon, I.J. and Illius, A.W. (1989). Resource partitioning by ungulates on the Isle of Rhum. *Oecologia* 79: 383-389.
- Gotelli, N.J. and Graves, G.R. (1996). *Null models in ecology*. Smithsonian Institution Press, Washington DC.
- Govender, N., Trollope, S.S.W. and Van Wilgen, B.W. (2006). The effect of fire season, fire frequency, rainfall and management on fire intensities in savanna vegetation in South Africa. *Journal of Applied Ecology* 43: 748-758.
- Gureja, N. and Owen-Smith, N. (2002). Comparative use of burned grassland by rare antelope species in a lowveld ranch, South Africa. *South African Journal of Wildlife Research* 32: 31-38.
- Hartnett, D.C., Hickman, K.R. and Fischer Walter, L.E. (1996). Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* 49: 413-420.
- Hobbs, N. T., Schimel, D. S., Owensby, C. E., and Ojima, D. S. (1991). Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72: 1374-1382.
- Hutchinson, G.E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* 93: 145-159.
- Jarman, P.J. (1974). The social organization of antelopes in relation to their ecology. *Behaviour* 48: 215-266.
- Jensen, M., Michelsen, A. and Gashaw, M. (2001). Responses in plant, soil inorganic and microbial nutrient pools to experimental fire, ash and biomass addition in a woodland savanna. *Oecologia* 128: 85-93.
- Laclau, J. P., Sama-Poumba, W., De Dieu Nzila, J., Bouillet, J. P. and Ranger, J. (2002). Biomass and nutrient dynamics in a littoral savanna subjected to annual fires in Congo. Acta *Oecologica* 23: 41-50.
- MacArthur, R.H. and Levins, R. (1967). The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* 101: 377-385.

McDowell, L.R. (1985). Nutrition of grazing ruminants in warm climates. Acedemic Press, Orlando.

- Menaut, J.-C., Abbadie, L. and Vitousek, P.M. (1993). Nutrient and organic matter dynamics in tropical ecosystems. Pp. 215-231 in Crutzen, P.J. and Goldammer, J.G. (eds.) *The ecological, atmospheric and climatic importance of vegetation fires*. John Wiley and Sons, Chichester.
- Moe, S. R. and Wegge, P. (1997). The effects of cutting and burning of grass quality and axis deer (Axis axis) use of grassland in lowland Nepal. *Journal of Tropical Ecology* 13: 279-292.
- Moe, S. R., Wegge, P. and Kapela, E. B. (1990). The influence of man-made fires on large wild herbivores in Lake Burungi in northern Tanzania. *African Journal of Ecology* 28: 35-43.
- Murray, M.G. and Illius, A.W. (1996). Multispecies grazing in the Serengeti. Pp. 247-272 in Hodgson, J. and Illius, A.W. (eds.) *The ecology and management of grazing*. CAB International, Wallingford.
- Ojima, D.S., Schimel, D.S., Parton, W.J. and Owensby, C.E. (1994). Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* 24: 67-84.
- Olff, H., Ritchie, M.E. and Prins, H.H.T. (2002). Global environmental controls of diversity in large herbivores. *Nature* 415: 901-904.
- Parr, C.L. and Andersen, A.N. (2006). Patch mosaic burning for biodiversity conservation : a critique of the pyrodiversity paradigm. *Conservation Biology* 20: 1610-1619.
- Pérez-Barberia, F.J., Elston, D.A., Gordon, I.J. and Illius, A.W. (2004). The evolution of phylogenetic differences in the efficiency of digestion in ruminants. *Proceedings of the Royal Society of London B: Biological Sciences* 271: 1081-1090.
- Prins, H.H.T. (1996). Ecology and behaviour of the African buffalo: social inequality and decision making. Chapman and Hall, London.
- Prins, H.H.T. and Olff, H. (1998). Species-richness of African grazer assemblages: towards a functional explanation. Pp. 449-490 in Newbery, D.M., Prins, H.H.T. and Brown, N. (eds.) *Dynamics of tropical communities*. Blackwell Science, Oxford.
- Putman, R.J. (1996). Competition and resource partitioning in temperate ungulate assemblies. Chapman and Hall, London.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. and

Zambatis, N. (2005). Determinants of woody cover in African savannas. *Nature* 438: 846– 849.

- Sankaran, M., Ratnam, J. and Hanan, N. (2008). Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17: 236-245.
- Schoener, T.W. (1974). Resource partitioning in ecological communities. Science 185: 27-39.
- Scholes, R.J. (1990). The influence of soil fertility on the ecology of southern African dry savannas. Journal of Biogeography 17: 415-419.
- Scholes, R.J. and Archer, S.R. (1997). Tree–grass interactions in savannas. *Annual Review of Ecology* and Systematics 28: 517–544.
- Singh, R. H. (1993). Effect of winter fire on primary productivity and nutrient concentration of dry tropical savanna. *Vegetatio* 106: 63-71.
- Tainton, N.M. (ed.) (1999). *Veld management in South Africa*. University of Natal Press, Pietermaritzburg.
- Tomor, B. M. and Owen-Smith, N. (2002). Comparative use of grass regrowth following burns by four ungulate species in Nylsvlei Nature Reserve, South Africa. *African Journal of Ecology* 40: 201-204.
- Trollope, W.S.W. (1999). Veld burning. Pp. 217-245 in Tainton, N.M. (ed.) *Veld management in South Africa*. University of Natal Press, Pietermaritzburg.
- Trollope, W.S.W., Biggs, H.C., Potgieter, A.L.F. and Zambatis, N. (1995). A structured vs. a wilderness approach to burning in Kruger in South Africa. Pp. 574-575 in West, N.E. (ed.) *Rangelands in a sustainable biosphere, Proceedings of the Fifth International Rangeland Congress, 1995.* Society for Range Management, Denver.
- Van de Vijver, C.A.D.M., Poot, P. and Prins, H.H.T. (1999). Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plant and Soil* 214: 173-185.
- Van Wilgen, B.W., Trollope, W.S.W., Biggs, H.C., Potgieter, A.L.F. and Brockett, B.H. (2003). Fire as a driver of ecosystem variability. Pp. 149-170 in Du Toit, J.T., Rogers, K.H. and Biggs, H.C. (eds.) *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington.
- Van Soest, P.J. (1982). Nutritional ecology of the ruminant. O and B Books, Corvallis.

Wilsey, B. J. (1996). Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology* 34: 32-38.