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Chapter 3

Fires and forage quality: the effects of burning regime on savanna regrowth quality

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ABSTRACT

Burning of tropical savanna grasslands is common practice in order to stimulate new regrowth for wildlife and livestock. To assess the effects of fire seasonality on the quality of post-fire regrowth as a food source for grazing herbivores, a burning experiment was set up in a moist savanna in north Cameroon. The experimental plots were burned either early, middle or late in the dry season, with the control plots left unburned. Regrowth quality was measured by concentrations of macronutrients (nitrogen, phosphorus, potassium, calcium, magnesium), digestibility, and parameters of sward structure such as green leaf biomass. The results of the experiment rejected our null hypothesis that nutrient levels, digestibility and sward structure are independent of fire seasonality. Burning increased nitrogen levels and digestibility, with the greatest effects in the middle of the dry season. The concentrations of calcium and magnesium were not affected, whereas potassium levels in the grass sward met herbivore requirements regardless of burning regime. Differences in sward structure were not an effect of the burning regime per se but of the ageing of the grass sward. All fire-induced changes in the grass sward only lasted during the dry season. Except for the removal of dead stems from the grass sward, burning late in the dry season had little value in providing nutritious forage for herbivores since the effects of burning were overridden by the effects of the first rains. During the dry season the protein contents and digestibility of unburned grass swards were structurally below the minimum requirements of ruminants. By raising nitrogen levels and digestibility above the maintenance levels of herbivores, fires thus enable grazing herbivores to survive the dry season on grass that would otherwise be of insufficient food quality.

3.1 INTRODUCTION

Prescribed burning is used as a management tool in many of the world's grassland ecosystems. Hundreds of millions of hectares of savanna areas are burned annually (Hao *et al.* 1990), making tropical C₄ grasslands the most frequently and extensively burned biome in the world (Hao & Liu 1994, Barbosa *et al.* 1999, Bond *et al.* 2005). Most fires occur in sub-Saharan Africa, where savanna fires account for nearly two-thirds of the global burned area (FAO 2007).

Although fires can result from natural causes such as lightning, the far majority of present-day bush fires are of anthropogenic origin (Bond & Van Wilgen 1996). Fires are lit for a multitude of reasons, including land clearance for agriculture, providing fire breaks around fields or villages, and clearing paths (Laris 2002). However, one of the main purposes of burning savanna grasslands is to provide regrowth for wildlife and livestock (e.g., Whelan 1995, Trollope 1999). Burning replaces old standing vegetation by palatable off-season regrowth which can sustain grazing herbivores such as cattle during the dry season. In this way prescribed burning of grasslands is used as a management tool for e.g. the renewal of pastures for pastoralists (Kull 2004), providing forage to wild bovids during periods of food scarcity (Wright 1974) and manipulating the grazing distribution of livestock (Vermeire *et al.* 2004).

Burning of savanna grasslands has important consequences for the quality and structure of the grass sward as forage for grazing herbivores. Concentrations of some macronutrients such as nitrogen, phosphorus and potassium in post-fire regrowth are generally higher than in unburned vegetation (Christensen 1977, Boerner 1982, Singh 1993, Van de Vijver *et al.* 1999, Laclau *et al.* 2002), although in East Africa nutrient levels have been shown to decline within three months to the levels of unburned vegetation (Van de Vijver *et al.* 1999). In addition, fires increase digestibility and alter the structure of the grass sward by increasing leaf:stem ratios and live:dead proportions (Van de Vijver *et al.* 1999). Because of the improved structure and quality of burned grass swards, grazing herbivores are able to reach higher forage intake rates on post-fire regrowth compared to unburned areas due to increased foraging efficiency (Drescher 2003, Hobbs *et al.* 1991, Moe & Wegge 1997). As a result, grazers tend to feed on grass regrowth following savanna fires rather than on 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, Klop & Van Goethem 2008).

The effects of fire on the grass sward are not straightforward, however, and depend on the fire regime that is applied, i.e, the frequency, intensity, and seasonality of burning. In temperate ecosystems, variation in burning seasonality has been shown to affect several vegetation characteristics (Coppedge *et al.* 1998, Howe 1994). Through vegetation, the fire regime can also affect grazing herbivores. Resource selection patterns of grazers are affected by fire-induced changes of the grass sward, such as regrowth age and the amount of dead stems in the sward (Klop *et al.* 2007). Grazing preferences of African herbivores are thus likely to be affected by the fire regime, as has also been shown for grazers in temperate grassland ecosystems (Coppedge & Shaw 1998). However, it is unclear to what extent fire seasonality affects the quality of the grass sward as a food source for grazing herbivores, especially on the nutrient-poor soils in the savannas of West Africa. Usually, West African savannas are burned at the onset of the dry season. In and around the national parks and hunting zones in the Guinea savanna of north Cameroon, the main reasons for burning at this time are 1) providing regrowth for wildlife and livestock during the season when grasses are dormant, 2) providing visibility to wildlife tourists and hunters who visit mostly during the dry season, and 3) avoiding uncontrolled mid- or late dry season fires that spread from surrounding villages or that are lit by poachers to mask illegal activities. In order to assess the effects of burning regime on regrowth quality for herbivores, in this paper we test the null hypothesis that the nutrient levels, digestibility and structure of the grass sward are independent of fire seasonality. This is done by means of a large-scale experiment in which different plots are burned at different times in the dry season. The consequences for grazing herbivores are then assessed by relating the quality and sward structure of burned and unburned grass swards to the food requirements of large grazers.

3.2 METHODS

Study area

This study was carried out in Bénoué National Park (1800 km²), located in the northern Guinea savanna belt (Stark & Hudson 1985) in north Cameroon. Annual rainfall ranges from 1200 to 1500 mm and is strongly unimodal with a wet season from April to October. Soils are ferruginous tropical (Brabant & Humbell 1974). Although the highest

point reaches up to over 1000 m, most of the terrain is characterised by low hills with two-thirds of the area between 300 and 450 m altitude. The dominant vegetation type is woodland savanna dominated by the tree *Isoberlinia doka* (Leguminosae–Caesalpinoideae) where the grass layer is dominated by *Andropogon* and *Hyparrhenia* spp. Along watercourses riparian forest dominated by *Anogeissus leiocarpus* (Combretaceae) is found. Other vegetation types are open savannas dominated by the tree genera *Terminalia* (Combretaceae), *Burkea* and *Detarium* (Leguminosae–Caes.) (Stark & Hudson 1985). The main grass species in the park belong to the genera *Andropogon*, *Hyparrhenia*, *Loudetia* and *Schizachyrium* (Verweij *et al.* 2006). Annual burning is concentrated in the months December to February, burning around 85% of the study area (Klop & Van Goethem 2008) although satellite imagery reveals that in some remote parts of the park the extent of burning is much lower (E. Klop, unpublished data).

Data collection

The effects of burning seasonality on vegetation quality and structure were tested by a burning experiment covering the entire dry season and the first half of the wet season. The field experiment followed a randomized complete block (RCB) design (Quinn & Keough 2002) with eight spatial units or replicas representing the blocks. The blocks were laid out over an area of c. 100 km², controlling for spatial effects such as soil fertility or soil water status. Each block consisted of four experimental plots (500–1000 m²) of which three received a burning treatment and one served as a control. The treatments consisted of early dry season burning (18 December 2004), mid dry season burning (12 February 2005) and late dry season burning (12 April 2005). The control plot was left unburned. After the late dry season burning in April, the number of blocks that could be sampled had to be reduced to four blocks because of a lack of manpower.

Vegetation measurements were done at regular four-week intervals at five randomly selected quadrats within each experimental plot, starting on 14 January and ending on 9 July 2005. The quadrat size was 0.25 m² on unburned plots but 1–2 m² on burned plots in order to extract enough material needed for the chemical analyses (see below). In these quadrats sward height was measured and the grass was clipped and air-dried. The dried grass samples were sorted into leaf and stem material and live (green) and dead (yellow) material and subsequently weighed. Samples of the green leaves were pooled per treatment per block and analysed on nutrient concentrations and

digestibility in a laboratory of Wageningen University, the Netherlands. In vitro digestibility was measured following the method of Tilley and Terry (1963) which imitates the digestion process of ruminants. Samples were incubated with rumen liquid, followed by incubation with a pepsin/HCl solution. Nutrient concentrations were measured after a modified Kjeldahl destruction. Concentrations of nitrogen (N) and phosphorus (P) were measured using a Skalar San-plus continuous flow autoanalyzer, whereas the concentrations of potassium (K), calcium (Ca) and magnesium (Mg) were analysed using an atomic absorption spectrometer.

Data analysis

The data were analysed using a general linear model (GLM) for a split-plot design, where treatment (burning regime) and block were between-subject factors and time (the monthly sample periods) was considered the within-subject factor that was crossed with treatment and block. The sward structure and quality parameters were the response variables. The following parameters of sward structure were included: sward height (cm), percentage green leaves of total green biomass, and green leaf bulk density, i.e., the amount of green leaf biomass per unit volume (g dm^{-3}). Bulk density is proportional to the amount of grass biomass a herbivore can obtain in a single bite, and was calculated as the green leaf biomass divided by the product of quadrat size, mean sward height and grass cover (%). Nutrient concentrations and digestibility were used as parameters of grass quality. Sward height and bulk density data were $\log_{10}$ transformed, whereas the percentages green leaf biomass were subjected to an arcsine transformation before analysis. The data of regrowth quality were left untransformed as they showed no strong deviation from normality.

The main null hypothesis of interest was that there is no effect of burning regime on grass quality and structure. Since regrowth quality is affected by the time elapsed since burning (Van de Vijver *et al.* 1999), we tested our hypothesis at two levels: 1) differences between treatments at any point in time, and 2) differences between treatments when correcting for differences in regrowth age. The second analysis was established by taking regrowth age as a covariate into the GLM. A multiple comparison of the main effects of burning regime was performed using post-hoc Tukey HSD tests to identify significantly different effects of different treatments. Any interactions of treatment with sample period or block were excluded from the multiple comparison analysis.

3.3 RESULTS

In the dry season, unburned grass swards had significantly lower nitrogen concentrations (mean: 0.71%, SD=0.34) than any of the burned swards (Table 1, Fig. 1a). Among treatments, N concentrations were significantly lower in swards that were burned early in the dry season (0.98%, SD=0.31) compared to swards that were burned mid-dry season (1.21%, SD=0.32), but there were no differences between early and late burned (1.12%, SD=0.42), or between mid-dry season and late burned swards (Table 2, Fig. 1a). Unburned swards also had significantly lower potassium concentrations (1.32%, SD=0.39) than swards that were burned early or mid-dry season (1.52%, SD=0.33) (Fig. 1c), but there were no differences with or between any of the other treatments. In addition, the nutrients calcium and magnesium did not show significant differences between any of the treatments in the dry season. Mean phosphorus concentrations in all treatments were around 0.11%, whereas mean calcium ranged from 0.37 to 0.43% and mean magnesium from 0.23 to 0.27% (Fig. 1b–e). None of the nutrients except potassium showed any differences between treatments in the wet season (Table 2).

Digestibility of the green leaves in unburned (mean: 50.2%, SD=7.5) swards was significantly lower than in swards that were burned early (57.1%, SD=7.3) or mid-dry season (57.8%, SD=9.6) (Fig. 1f). The green leaf fraction of the total green biomass was significantly lower in unburned vegetation (65.3%, SD=16.9) than in the early or mid-dry season burned swards, but there were no differences between the burned swards where the green leaf fraction ranged from 76.0 to 78.0% (Fig. 1g). Not surprisingly, the mean sward height was highest in unburned vegetation. However, the effects of burning regime on sward height and percentage green leaves disappeared when correcting for regrowth age. Mean bulk density of the green leaf fraction varied from 1.0 g dm⁻³ (SD=0.8) for early burned to 1.2 g dm⁻³ (SD=0.9) for mid-dry season burned and 1.6 g dm⁻³ (SD=1.2) for late burned swards, compared to 8.0 g dm⁻³ (SD=71.7) for unburned swards. However, we could not find any significant differences between the log₁₀ transformed values of green leaf bulk density for any of the treatments (Table 1,2, Fig. 1h).

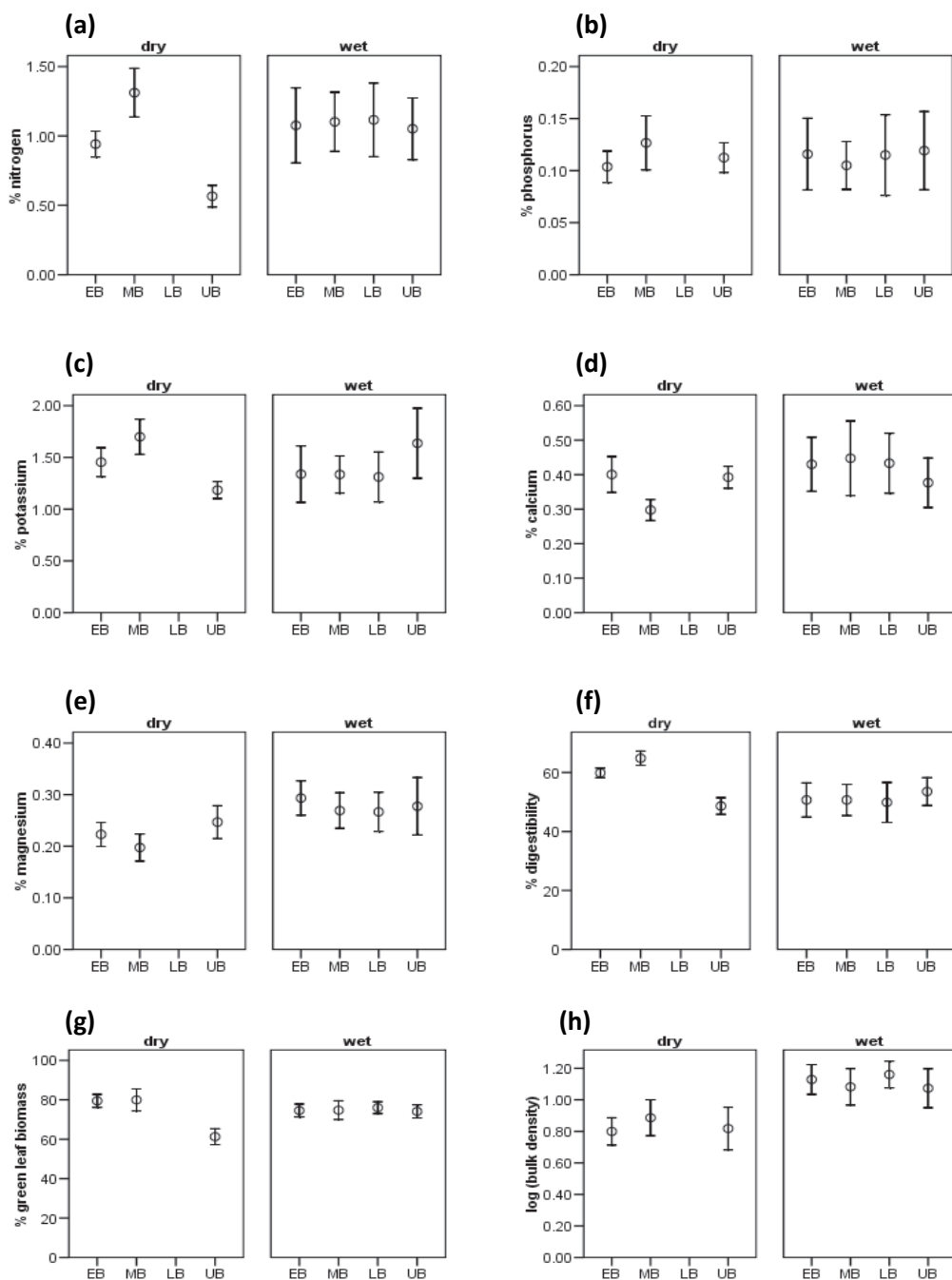


Fig. 1. Mean values and associated 95% confidence intervals of the sward quality and structure parameters for early dry season burning (EB), mid-dry season burning (MB), late dry season burning (LB) and unburned (UB) treatments. The graphs are split into data from the dry (January–April) and early wet season (May–July).

The effects of sample period were significant for nearly all parameters of structure and quality (Table 1,2). All variables except calcium and magnesium had significant treatment by month interactions, i.e., the effects of treatment differed per sample period. In addition, treatment by block interactions were found for all variables of sward structure but not for the quality parameters. Only magnesium showed a significant main effect of block, in the wet season.

Table 1. Effects of burning regime (treatment) on sward quality and structure during the dry season. The multiple comparison shows significant differences at $P < 0.05$ between early dry season burning (EB) mid-dry season burning (MB), late dry season burning (LB) and unburned (UB). The last column lists any effects of block, time (month) or any interactions between block, time and treatment that are significant at $P < 0.05$.

Parameter	At any point in time		Corrected for regrowth age		Multiple comparison	Significant effects
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>		
Nitrogen (N)	61.69	0.00	19.79	0.00	UB < EB < MB	Month, treatment × month
Phosphorus (P)	4.38	0.03	9.50	<0.01	-	Month, treatment × month
Potassium (K)	49.01	0.00	17.10	0.00	UB < EB < MB	Month, treatment × month
Calcium (Ca)	2.01	0.17	2.84	0.10	-	-
Magnesium (Mg)	0.46	0.64	0.05	0.82	-	Treatment × block, month × block
Digestibility	44.32	0.00	6.14	0.02	UB < EB < MB	Treatment × month
Log (sward height)	22.93	0.00	0.08	0.77	EB, MB < UB	Month, treatment × month, treatment × month × block
Arcsin (% green leaves)	17.18	0.00	1.23	0.28	UB < EB, MB	Month
Log (green leaf bulk density)	2.00	0.17	4.12	0.06	-	Treatment × month, treatment × block, month × block, treatment × month × block

Table 2. Effects of burning regime (treatment) on sward quality and structure during the first half of the wet season (May–July). For details see Table 1.

Parameter	At any point in time		Corrected for regrowth age		Multiple comparison	Significant effects
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>		
Nitrogen (N)	0.80	0.52	0.20	0.82	-	Month, treatment × month, treatment × block
Phosphorus (P)	0.62	0.62	0.60	0.57	-	Month
Potassium (K)	6.73	0.01	0.19	0.83	EB, MB, LB < UB	Month, treatment × month
Calcium (Ca)	0.85	0.50	0.10	0.90	-	Month, treatment × month, treatment × block
Magnesium (Mg)	0.33	0.80	0.47	0.64	-	Block, treatment × month, treatment × block
Digestibility	0.77	0.54	0.02	0.99	-	Month
Log (sward height)	9.74	<0.01	1.06	0.39	EB, MB, LB < UB	Month × block
Arcsin (% green leaves)	0.17	0.92	0.11	0.89	-	Treatment × month × block
Log (green leaf bulk density)	1.16	0.38	0.96	0.42	-	Month, month × block

3.4. DISCUSSION

The results of the burning experiment reject our hypothesis that nutrient levels, digestibility and structure of the grass sward are independent of fire seasonality. Mid-dry season burning resulted in higher concentrations of nitrogen and potassium and higher digestibility of the grass sward than early burned swards, which in turn had higher N and K concentrations and digestibility than unburned swards. However, the differences in sward quality between any of the treatments only lasted during the dry season and disappeared during the wet season.

The main importance of the burning regime to herbivore forage quality lies in the dry season levels of leaf tissue nitrogen and digestibility of the plant material.

Ruminants need a minimum of 5–7% crude protein in their food to support rumen fermentation (Van Soest 1982, 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 with sub-maintenance levels in unburned vegetation. Burning in the Guinea savanna thus enables grazing herbivores to survive the dry season on grass of which the quality would otherwise be below herbivore maintenance levels. During the wet season nitrogen levels were independent of burning regime and sufficient in all treatments. Likewise, during the wet season both burned and unburned swards met the minimum maintenance levels for domestic bovids of around 50% digestibility, but during the dry season only the burned swards had digestibility values of around 60% that are required by lactating animals (Van Soest 1982).

The burning regime 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 the burning regime, in all treatments the potassium levels were above the minimum requirements for domestic bovids which range from 0.50 to 0.80% with values up to 1.20% for lactating dairy cattle. Calcium and magnesium concentrations were not affected by the burning regime. Calcium is an element important in determining the spatial distribution of ungulates (McNaughton 1988). The observed levels in all treatments fell within the range of minimum calcium requirements (0.20–0.60%) for domestic bovids. However, metabolic requirements of calcium, phosphorus and vitamin D are closely related and a deficiency or excess of one will likely interfere with the proper utilization of the other (McDowell 1985). The Ca:P ratios of 3.4:1 to 3.9:1 that were found in the grass swards seem rather wide compared to ratios of 1:1 or 2:1 that are recommended for cattle feed, but the observed ratios fall well within the tolerance range of ruminants (McDowell 1985). Magnesium requirements range from 0.04 to 0.20% for domestic ruminants, which are well below the observed concentrations in burned and unburned swards. However, magnesium absorption in the rumen–reticulum can be impaired by several other nutrients, in particular high concentrations of potassium and nitrogen which increase gut passage rate (McDowell 1985).

Although differences in green leaf biomass were not the result of the burning regime per se but of the ageing of the grass sward, this does not mean that from a herbivore's point of view the structure of burned and unburned swards are the same. An important effect of burning is removing the dead grass biomass that reduces access and

bite mass of grazing herbivores (Drescher 2003). Thus even when the green leaf biomass remains unchanged, burning makes the green biomass more accessible to herbivores.

The effects of burning late in the dry season were largely undone by the rains that immediately followed the late burning treatment (78 mm between 16 and 30 April). Although in the wet season potassium levels and sward height of burned swards were significantly different from unburned swards, these differences were the effect of ageing rather than the burning regime (Table 2). During the wet season, nutrient concentrations in unburned swards matched those of burned swards. In addition to increased rates of photosynthesis and nutrient uptake because of high moisture availability, leaf tissue nutrient levels in the wet season may also be increased through enhanced soil nutrient availability as a result of increased mineralization rates, increased decomposition rates of dead plant material, wet deposition and (on burned plots) leaching of nutrients from ashes into the soil. Since soil microbial activity is strongly moisture dependent (Holt & Coventry 1990), rainfall is the principal factor affecting nitrogen mineralization rates and the first rains after the dry season can lead to sudden bursts in mineralization rates (Scholes *et al.* 2003). In addition, the rain induced regrowth leads to changes in sward structure such as increases in height, green leaf biomass and bulk density.

Management implications

Our results agree with previous research, where burning increased the nutrient concentrations in post-fire regrowth (Christensen 1977, Frost and Robertson 1987, Hobbs *et al.* 1991, Singh 1993, Van de Vijver *et al.* 1999, Laclau *et al.* 2002). However, our study shows that the effects of burning are strongly dependent on the season in which burning activity takes place. These findings have important consequences for the fire management in protected areas. Most management fires in Bénoué N.P. are lit in December and January, with sporadic burning activity afterwards. Based on the data presented in this paper and on herbivore resource selection on post-fire regrowth (Klop *et al.* 2007), a longer fire season is recommended in which burning activity is spread out more evenly over the dry season. This should ensure the availability of high-quality grass swards throughout the dry season. Although mid-dry season burning resulted in higher concentrations of nitrogen and potassium and higher digestibility of the grass sward than early burned swards, 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.

REFERENCES

- 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.
- Barbosa, P.M., Grégoire, J.-M. and Pereira, J.M.C. (1999). An algorithm for extracting burned areas from time series of AVHRR GAC data applied at a continental scale. *Remote Sensing of Environment* 69: 253-263.
- Boerner, R.E.J. (1982). Fire and nutrient cycling in temperate ecosystems. *Bioscience* 32: 187-191.
- Bond, W.J. and Van Wilgen, B.W. (1996). *Fire and plants*. Chapman and Hall, London.
- Bond, W.J., Woodward, F.I. and Midgley, G.F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525-538.
- Brabant, P. and Humbel, F.X. (1974). *Notice explicative de la carte pédologique de Poli, No 51*. ORSTOM, Paris.
- 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.
- Coppedge, B.R. and Shaw, J.H. (1998). Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Range Management* 51: 258-264.
- Coppedge, B.R., Engle, D.M., Toepfer, C.S. and Shaw, J.H. (1998). Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecology* 139: 235-246.
- Drescher, M. (2003). *Grasping complex matter: large herbivore foraging in patches of heterogeneous resources*. PhD thesis, Wageningen University, Wageningen.
- FAO (2007). *Fire management – global assessment 2006*. FAO Forestry Paper 151, FAO, Rome.
- Frost, P.G.H. and Robertson, F. (1987). The ecological effects of fire in savannahs. Pp. 93-140 in Walker, B.H. (ed.) *Determinants of tropical savannahs*. IRL press, Oxford.

- 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.
- Hao, W.M. and Liu, M.H. (1994). Spatial and temporal distribution of tropical biomass burning. *Global Biochemical Cycles* 8: 485-503.
- Hao, W.M., Liu, M.H. and Crutzen, P.J. (1990). Estimates of annual and regional releases of CO₂ and other trace gases to the atmosphere from fires in the tropics, based on the FAO statistics for the period 1975-1980. Pp. 440-462 in Goldammer, J.G. (ed.) *Fire in the tropical biota: ecosystem processes and global challenges*. Ecological Studies 84, Springer Verlag, Berlin.
- 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.
- Holt, J.A. and Coventry, R.J. (1990). Nutrient cycling in Australian savannas. *Journal of Biogeography* 17: 427-432.
- Howe, H.F. (1994). Response of early- and late-flowering plants to fire season in experimental prairies. *Ecological Applications* 4: 121-133.
- Klop, E. and Van Goethem, J. (2008). Savanna fires govern community structure of ungulates in Bénoué National Park, Cameroon. *Journal of Tropical Ecology* 24: 39-47.
- Klop, E., Van Goethem, J. and De longh, H.H. (2007). Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research* 34: 77-83.
- Kull, C.A. (2004). *Isle of fire: the political ecology of landscape burning in Madagascar*. The University of Chicago Press, Chicago.
- 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.
- Laris, P. (2002). Burning the seasonal mosaic: preventative burning strategies in the wooded savanna of southern Mali. *Human Ecology* 30: 155-186.
- McDowell, L.R. (1985). *Nutrition of grazing ruminants in warm climates*. Academic Press, Orlando.
- McNaughton, S.J. (1988). Mineral nutrition and spatial concentrations of African ungulates. *Nature* 334: 343-345.
- 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.
- Prins, H.H.T. (1996). *Ecology and behaviour of the African buffalo: social inequality and decision making*. Chapman and Hall, London.
- Quinn, G.P. and Keough, M.J. (2002). *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge.
- Scholes, M.C., Scholes, R.J., Otter, L.B. and Woghiren, A.J. (2003). Biogeochemistry: the cycling of elements. Pp. 130-148 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.
- Singh, R.H. (1993). Effect of winter fire on primary productivity and nutrient concentration of dry tropical savanna. *Vegetatio* 106: 63-71.
- Stark, M.A. and Hudson, R.J. (1985). Plant communities in Bénoué National Park, Cameroon: a cluster association analysis. *African Journal of Ecology* 23: 21-27.
- Tilley, J.M.A. and Terry, R.R. (1963). A two-stage technique for the in vitro digestion of forage crops. *Journal of the British Grassland Society* 18: 104-111.
- 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.
- 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 der Zon, A.P.M. (1992). *Graminées du Cameroun*. Wageningen Agricultural University Papers, Wageningen.
- Van Soest, P.J. (1982). *Nutritional ecology of the ruminant*. O & B Books, Corvallis.
- Vermeire, L.T., Mitchell, L.B., Fuhlendorf, S.D. and Gillen, R.L. (2004). Patch burning effects on grazing distribution. *Journal of Range Management* 57: 248-252.
- Verweij, R.J.T., Verrelst, J., Loth, P.E., Heitkönig, I.M.A. and Brunsting, A.M.H. (2006). Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. *Oikos* 114: 108-116.
- Whelan, R.J. (1995). *The ecology of fire*. Cambridge University Press, Cambridge.

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.

Wright, H.A. (1974). Range burning. *Journal of Range Management* 27: 5-11.