

Dynamics of Sudanian Savanna-Woodland Ecosystem in Response to Disturbances

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Cover photo: Coppices, herbivory and fire in the savanna-woodland of Burkina Faso
(Taken by P. Savadogo)

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Abstract

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Grazing, fire and selective tree cutting are major disturbances shaping species diversity and productivity in savanna-woodland ecosystems. Their effects, however, are highly variable and poorly understood. Structural and functional responses of the Sudanian savanna-woodland ecosystem to such disturbances were investigated, with particular emphasis on the herbaceous vegetation.

Fuel and fire behaviour were characterized in relation to grazing, dominant grass type and wind direction. The results indicated that fuel consumption by fire was significantly reduced by moderate livestock grazing intensity; rate of spread was faster and flame height shorter in head fire than back fire. The average maximum temperature was high on: non-grazed areas; areas dominated by annual grasses; plots subjected to head fire; and at the soil surface. Residence time of temperatures above 60°C, considered lethal for plant tissues, exhibited a similar trend to that for fire temperature. Examination of structural responses of herbaceous vegetation to disturbances revealed that grazing favoured the diversity of perennial grasses. Fire favoured annual and perennial grasses richness. Selective cutting had no effect on any of the vegetation attributes assessed. The combined effect of grazing, fire and selective cutting increased the diversity of forbs. Structural responses exhibited significant temporal variation, which could be related to inter-annual variation in rainfall, stocking rate and fire intensity. Principal Response Curves analysis provided further evidence that their effects were species-specific. Functional responses of the ecosystem were characterized by soil physico-chemical and hydrological properties, aboveground biomass production and chemical concentration. High grazing intensity reduced soil water infiltration and aboveground biomass through increased trampling and herbage removal. Annual early fire tended to reduce steady state infiltration rate due to its effect on soil organic matter that explained 34% of the steady state infiltration rate. Long-term frequent fire affected neither soil physico-chemical properties nor total aboveground herbaceous biomass. Further analysis of fire effects on biomass production and nutrient composition of four grass species indicated that it significantly reduced above-ground dry matter, crude protein, neutral detergent insoluble crude protein and Ca, Fe, and Mn concentrations.

In conclusion, moderate grazing intensity could be used to modify fire behaviour, to reduce susceptibility to erosion and to maintain sufficient biomass production. For vegetation management, back fires are recommended as they are less intense. The variation in structural responses between sites highlights the importance of landscape-scale approaches for understanding the impacts of disturbances on Sudanian savanna-woodland ecosystems that seems to follow the non-equilibrium theory of disturbance dynamics.

Keywords: Fire; herbivory; selective tree cutting; biomass production; herbaceous diversity; soil water infiltration; nutrient contents; Burkina Faso, West Africa.

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Paper I-V

This thesis is based on the following papers, which will be referred to in the text by their corresponding roman numerals.

- I. Patrice Savadogo, Didier Zida, Louis Sawadogo, Daniel Tiveau, Mulualet Tigabu and Per Christer Odén. 2007. Fuel and fire characteristics in a savanna-woodland of West Africa in relation to grazing and dominant grass type. (Submitted manuscript).
- II. Patrice Savadogo, Daniel Tiveau, Louis Sawadogo and Mulualet Tigabu. 2007. Herbaceous species responses to long-term effects of prescribed fire, grazing and selective tree cutting in the savanna-woodland of West Africa. (Submitted manuscript).
- III. Patrice Savadogo, Mulualet Tigabu and Louis Sawadogo. 2007. Multivariate analysis of dynamic responses of herbaceous vegetation communities to disturbances in the Sudanian savanna-woodland using Principal Response Curves. (Manuscript).
- IV. Patrice Savadogo, Louis Sawadogo and Daniel Tiveau. 2007. Effects of grazing intensity and prescribed fire on soil physical and hydrological properties and pasture yield in the savanna woodlands of Burkina Faso. *Agriculture Ecosystems & Environment*, 118: 80-92.
- V. Patrice Savadogo, Mulualet Tigabu, Louis Sawadogo and Per Christer Odén. 2007. Dry matter production and nutrient composition of four grass species in a Sudanian savanna-woodland subjected to repeated early fire. (Submitted manuscript).

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Introduction

Background

African dry forests and woodlands cover vegetation types dominated by a continuous tree cover (70%), experiencing drought more than three months each year (Menaut, Lepage & Abbadie, 1995), and occurring within the savanna biome (Scholes & Walker, 1993; Breman & Kessler, 1995). They cover approximately 43% of the continent or 13 million km², and are divided into two distinct regions; the northern hemisphere (Sudanian region) and the southern hemisphere (Zambezian region). The Sudanian savanna-woodland comprises an area stretching from Senegal in the west to the Ethiopian highlands in the east, between 6° and 13° N, covering an area of 5.25 million km² (Menaut, Lepage & Abbadie, 1995). In West Africa, the savanna-woodlands stretch between the tropical Guinea Forest and the semi-desert and desert of the Sahara (Cole, 1986).

Savanna vegetation varies considerably in its structure and is characterized by mixtures of scattered trees or scattered clumps of trees and drought-resistant grasses (Bourliere & Hadley, 1983; Cole, 1986; Scholes & Walker, 1993). Vegetation patterns, dynamic processes and species diversity in the Sudanian savannas are often attributed to environmental heterogeneity (Menaut, Lepage & Abbadie, 1995; Bellefontaine, Gaston & Petrucci, 2000). For example, in West Africa large termitaria have an important effect on community structure in terms of spatial distribution, density and diversity of trees (Konaté *et al.*, 1998). Savannas with a high density of trees and shrubs are confined to areas dominated by ferruginous soils, while savannas with low tree and shrub density are confined to areas with brown loamy soils (Menaut, Lepage & Abbadie, 1995).

In addition, factors such as soil moisture and nutrient status, and disturbances such as fire and herbivory affect the structure and functions of tropical savannas (Bourliere & Hadley, 1983; Scholes & Archer, 1997; Higgins, Bond & Trollope, 2000; Sankaran, Ratnam & Hanan, 2004; Bond, 2005). Soil moisture and nutrient availability affect the relative abundance of grasses and woody plants, the patterns of primary production and plant quality. These in turn influence the type and extent of herbivory and any associated animal impact, as well as the frequency and intensity of fire. Anthropogenic activities have influenced the structure of African savannas for more than two millions years (Harris, 1980). Humans affect savanna structure either directly through wood cutting and cultivation, or indirectly through their ability to manipulate fire and influence herbivore numbers and distribution, both by hunting and by introducing and managing livestock (Frost *et al.*, 1986).

Disturbances in savanna-woodland ecosystem

Disturbance is generally defined as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource pools, substrate availability, or the physical environment (White & Pickett, 1985). It may be natural or anthropogenic in origin (Turner *et al.*, 2003) and may lead to

sudden or gradual, dramatic or subtle changes in ecosystems (White & Jentsch, 2001). Disturbances are ubiquitous, inherent and unavoidable and affect all levels of biological organization from individuals to ecosystems and landscapes with different consequences and mechanisms at each hierarchical level (Rykiel, 1985). They are primary causes of patchiness and heterogeneity in ecosystems (Turner *et al.*, 2003) and are evolutionary forces causing adaptation in the biota exposed to them (Darwin, 1859; McNaughton, 1983; van Langevelde *et al.*, 2003). The effects of disturbances are often contingent on the frequency, intensity and timing of their interactions, on the past and present states of the system and their interaction with future events (Frost *et al.*, 1986). The orthodox view adheres to the equilibrium theory, which postulates that once disturbance occurs in a system (e.g. a vegetation community), the system's state either returns to its former equilibrium or equilibrates within a new "domain of attraction" (Tainton, Morris & Hardy, 1996). Generally, following disturbances some species may increase or invade while other decrease or retreat (Gibson & Brown, 1991). Such functional adaptations underlie two mechanisms of ecosystem response to disturbances; namely complementarity and redundancy (Walker, 1992), that contribute to ecosystem stability and resilience. Ecosystem stability is the probability of all species persisting and is enhanced if each main functional group of organisms (important for maintaining function and structure) comprises several ecologically equivalent species, each with different responses to environmental factors (Walker, 1995). Ecosystem resilience is the ability of an environment to tolerate stresses and maintain its life-supporting capacity without shifting to a different state (Walker, 1995; Mercedes & Guichard, 2005). Ecosystem resilience is an integral part of sustainable development for numerous economic, social and cultural reasons (Adger, 2000). Therefore, improving our understanding of the effects of disturbances on land would facilitate ecologically informed management decisions (Turner *et al.*, 2003). The conceptual framework of disturbance regimes in savanna-woodland is presented in Fig. 1 and the effects of each major disturbance regime are reviewed below.

Fire

Fire has been an important ecological feature of African savanna ecosystems for millennia and seems to have acted not only as a destructive force but also as selective and regulatory agent (Goldammer, 1990; Scholes & Walker, 1993; van Langevelde *et al.*, 2003). In the Sudanian Zone, it is estimated that 25 to 50% of the area burns annually (Delmas *et al.*, 1991), and the entire zone burns every 2-3 years mainly as a result of human activity (Menaut, Lepage & Abbadie, 1995). For many African farmers fire is an essential and cheap tool for hunting, clearing unwanted vegetation, maintaining grasslands and removing dry vegetation and crop residues to promote agricultural productivity and allow greater visibility (Ehrlich, Lambin & Malingreau, 1997; Laris & Wardell, 2006). Most fires occur at the start of the dry season when herbaceous biomass has dried out.

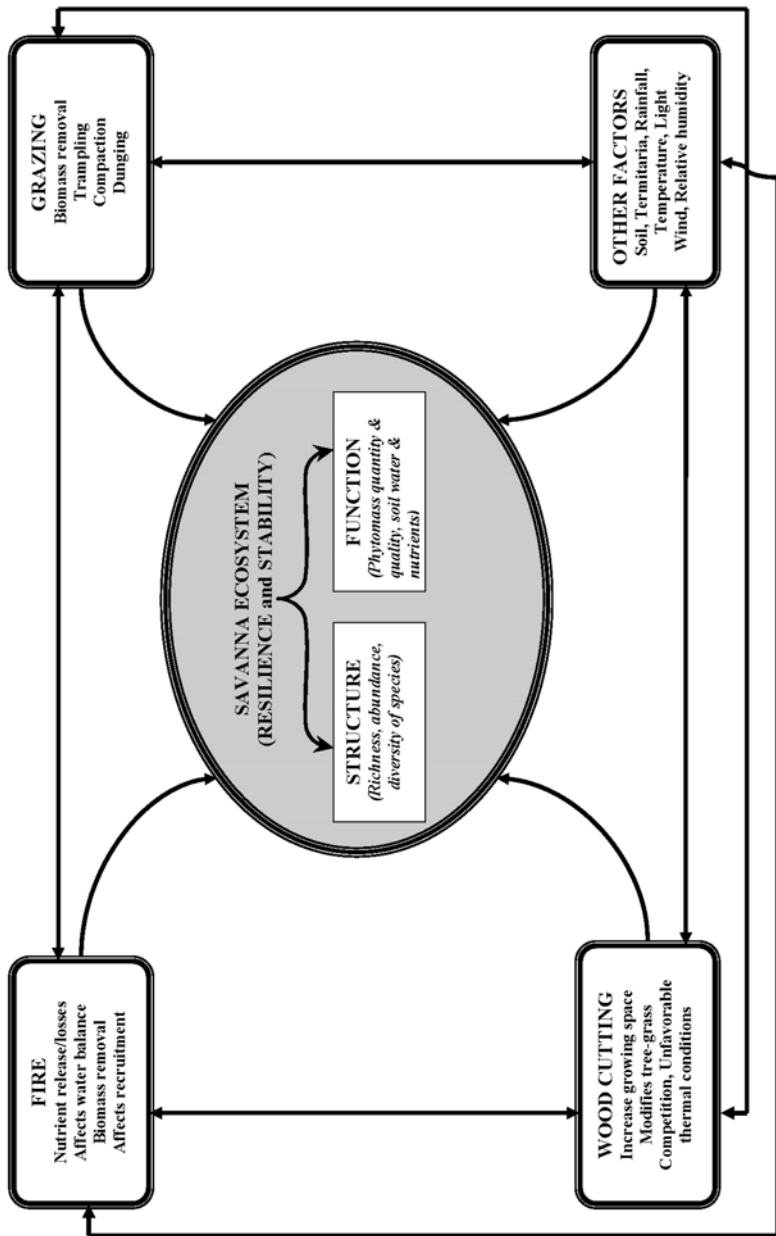


Fig. 1. A simplified conceptual framework of effects of disturbances and their interactions on structure and function of savanna-woodland ecosystem

Fire is known to shape savanna biomes (Bond & van Wilgen, 1996; van Langevelde *et al.*, 2003). Virtually all savanna vegetation communities exhibit evidence of fire dependence or tolerance (Frost *et al.*, 1986; Swaine, 1992). Plant species differ in their response to fire (Table 1); some are entirely resistant, others may have their above ground biomass destroyed but are able to sprout from underground organs after fire, while a third group are reliant to seed for recovery (Bond & van Wilgen, 1996). In most tropical savannas, frequent fires consume the accumulated grass production and litter and favour the development and maintenance of a predominantly grassland vegetation by reducing the natural regeneration of trees and shrubs (Hoffmann, 1999). Fire can also stimulate and increase flowering and, thus, seed production among shrubs and herbaceous species (Baskin & Baskin, 1998). The germination of seeds of many plants species is dependant on fire providing one or more physical (temperature, light) and/or chemical (smoke, nutrients and gases) cues (Dixon, Roche & Pate, 1995; Brown & van Staden, 1997; van Staden *et al.*, 2000). Temporary suppression of fire is a human induced disturbance (Menaut *et al.*, 1991) because some herbaceous and woody species which are usually resistant in burnt areas become often weak in protected areas. Absence of fire may perturb their fecundity either by maintaining a dense layer of standing dead material which impedes young suckers, or by keeping alive buds on old axes and thereby weakening the plant (Menaut & Cesar, 1982).

Table 1. *Summary of responses to burning exhibited by various plant species and possible explanations for these responses (After Whelan, 1995)*

Observation	Possible explanation
Increased productivity	Increase nutrient availability Removal of suppressive dead leaves Increased average soil temperature Extended period of high temperature Earlier start to growing season
Increased flowering	Increase nutrient availability Increase in numbers of shoots sprouting Removal of competing vegetation
Increased seed dispersal distance	Removal of canopy around fruits Removal of ground vegetation and litter Greater foraging distance by seed dispersal agent
Synchrononous release of canopy-stored seeds	Heat treatment of sealed follicles or scales
Synchrononous release of soil-stored seeds	Heat treatment of impermeable seed coats Smoke and charcoal residues break dormancy Alter surface light and temperature regime
Improved establishment of seedlings	Increase nutrient availability Decrease herbivory activity Removal of competing vegetation Satiation of population of seed predators

Soil is an important component of ecosystems that is likely to be affected by fire. Fire related changes in soils may produce a wide array of changes in other ecosystem components as a result of their interdependency (DeBano, Daniel & Peter, 1998). Burning results in a short-term increase in soil available nitrogen and other mineral nutrients immediately after burning (Jensen, Michelsen & Gashaw, 2001; Wan, Hui & Luo, 2001), which in turn stimulates the growth of herbaceous vegetation. However, frequent fire may have a detrimental effect on soil physico-chemical properties by destroying the organic matter contained in the aboveground vegetation and litter (Bird *et al.*, 2000; Parker *et al.*, 2001). Therefore it may adversely affect nutrient pool sizes and fluxes by leaching and volatilization (Wan, Hui & Luo, 2001; Laclau *et al.*, 2002) and may kill soil fauna. Frequent burning increases the tendency of a soil to crust, increases runoff, decreases soil organic matter and stability of the aggregates, and reduces soil porosity and water infiltration rate (Mills & Fey, 2004).

The effects of fire on vegetation and soil depend on intensity and frequency, which are in turn influenced by a wide range of variables such as topography, fuel characteristics, vegetation structure, the season of burning, and weather conditions (Pyne, Patricia & Richard, 1996). Early fire is often less intense than late fire due to the relatively high moisture levels present in the fuel. Given its low intensity and the fact that it reduces the risk of accidental late fire by creating a spatially discontinuous (patchy) supply of herbaceous fuel (Delmas *et al.*, 1991; Chidumayo, 1997), early fire is employed as a management tool in many managed savanna ecosystems. Attitudes towards the use of fire as a management tool have ranged from pyromania to pyrophobia (Scholes & Walker, 1993) due to the nature of the constraints on its practical use in vegetation management (Bond & van Wilgen, 1996). Thus knowledge of the effects that fire has on vegetation, characterization of fire behaviour and development of fire behaviour prediction models are essential for judicious use of fire for savanna-woodland management.

Herbivory

In most parts of Africa, the herbaceous component of savanna-woodlands is essential as forage for domestic and wild animals and has other ecological and economic values. In the Sudanian Zone of West Africa, livestock rearing has, for centuries, been crucial in supporting the livelihoods of local people. The effect of herbivores on ecosystem processes and particularly their impact on vegetation succession can generally be divided into three categories: herbage removal, dunging (deposition of faeces and urine), and soil and litter trampling and compaction (Hiernaux *et al.*, 1999). The first and most obvious effect of herbivores is the removal of biomass (browsing and grazing) which is the main biotic factor affecting vegetation structure and dynamics (Belsky, 1992; Milchunas & Lauenroth, 1993; Diaz, Noy-Meir & Cabido, 2001; Bakker *et al.*, 2006). Grazing changes the arrangement of photosynthetic structure of communities according to the type of animal involved (Rook *et al.*, 2004). Selective grazing, as well as heavy stocking rate, may alter floristic composition and result in a shift from long-lived perennials to annuals and forbs, with a concomitant decrease in

production (Fuhlendorf, Briske & Smeins, 2001). Light grazing promotes the succession from grassland to woodland (Watkinson & Ormerod, 2001), while cessation of grazing has been found to lead to a decline in species diversity in pasture lands. Severe grazing, known as overgrazing, is defined as the situation when “forage species are not able to maintain themselves due to an excess of herbivory or related processes” (Holechek *et al.*, 1999). This can lead to the degradation of plant and soil resources, desertification (Keya, 1998) or the loss of species richness and an increased abundance of unpalatable species (Mwendera, Saleem & Woldu, 1997). Overgrazing is linked to the concept of a decline in carrying capacity (Mysterud, 2006) known as the maximum possible stocking of herbivores that rangeland can support on a sustainable basis (FAO, 1991).

Dunging by herbivores plays a key role in determining structure, functioning and dynamics of savanna ecosystems. Deposition of dung represents a potential source of soil nutrients (N, P, K and micronutrients) and improves soil physical and chemical properties (Harris, 2002; Cumming & Cumming, 2003; Rufino *et al.*, 2006). A significant increase in soil nutrients around dung patches was observed by MacDiarmid and Watkin (1972), this affected plant growth around the patch. Dung acts as a slow release fertilizer, providing nutrients through one or more growing seasons (Williams & Haynes, 1995; Harris, 2002) provided that it is not washed away. Dung also plays an important role in the dynamics of plant communities by smothering the areas where it is deposited; this could be detrimental to plant growth. Plant seedlings covered by dung may die due to lack of light (Williams & Haynes, 1995). Herbivores also play a key role in long distance dispersal of propagules (Milton & Dean, 2001), enhancing local colonization processes and plant diversity (Olf & Ritchie, 1998).

The hooves of grazing animals affect the vegetation by detaching or destroying plant material and by influencing the water regime as a result of soil compaction (Abdel-Magid, Trlica & Hart, 1987; Hansson, 2004). The type of animal, season and intensity of grazing, soil characteristics and plant communities present influence the type and degree of impact. Livestock grazing is often regarded as one of the main causes of vegetation and soil degradation in the Sudano-sahelian regions (Le Houerou, 1976; Lusigi & Glaser, 1984; Warren, Batterbury & Osbahr, 2001). Gaps created by trampling lead to unfavourable thermal conditions, thus increasing soil evaporation and plant evapotranspiration. Therefore, in order to use livestock as an effective management tool it is important to find a balance between the carrying capacity, the amount of livestock and the timing of livestock presence in the forests.

Wood cutting

Selective removal of trees influences structure and function of the savanna-woodland ecosystem in a variety of ways (see Fig. 1). Generally, canopy gaps created by tree removal are expected to result in increased diversity and abundance due to reduced competition for water and nutrients, as well as increased availability of light (Frost *et al.*, 1986). These factors are expected to contribute to

enhanced local colonization processes. In arid and semi-arid areas, however, the canopy gaps created by the selective removal of trees may result in unfavourable thermal conditions and favour the growth of drought-tolerant species, thereby contributing to competitive exclusion processes. In addition, as most savanna trees regenerate vegetatively post cutting disturbance (Sawadogo, Nygård & Pallo, 2002; Hoffmann & Solbrig, 2003; Ky-Dembele *et al.*, 2007), the compensatory response of trees may lead to increased competition for water and nutrients, adversely affecting the herbaceous vegetation. When tree density increases, grass production tends to decrease (Grunow, Groeneveld & Du Toit, 1980; Mordelet & Menaut, 1995) due to thermal interference (Ball *et al.*, 2002), shading and increased competition for water and nutrients. However, the opposite has sometimes been found (Belsky, 1994; Grouzis & Akpo, 1997) especially for isolated trees (Belsky *et al.*, 1989; Weltzin & Coughenour, 1990; Belsky, Mwonga & Duxbury, 1993). The roots of woody plants are fundamental in their competitive interactions with herbaceous species and other woody plants because they determine the spatial distribution of water and nutrient uptake and can cause an increase or a decrease in resource availability (Wu *et al.*, 1985). Grasses, with relatively shallow, dense, fibrous root systems, may actively compete with trees for resources, either directly by intercepting water and nutrients or indirectly by reducing percolation down the soil profile to where tree roots may be more abundant. The removal of trees, therefore, results in increased grass production but the total aboveground plant production usually decreases (Scholes & Walker, 1993).

Interactive effects of disturbances

Disturbances in ecosystems can act independently or additively (Belsky, 1992; Valone, Nordell & Ernest, 2002; Valone, 2003). Fire, herbivory, the overlying tree canopy and other environmental factors affect spatial patterns of diversity and community organization in savanna-woodlands (see Fig. 1). Generally, the co-occurrence of fire and grazing has a synergistic effect on plant communities both in time and space (McNaughton, 1983). Their effects depend on the growth form and physiological state of the plant species affected, season, frequency and intensity of burning, grazing pressure, physical structure of the landscape, and climatic conditions (Frost *et al.*, 1986; Coughenour, 1991). Many grazers are attracted to recently burnt ground to feed on post fire regrowth of grasses. Grazers in turn reduce the fuel load by consumption and trampling and therefore lower the intensity and frequency of fire. Selective cutting temporally provides more space and resources for the growth of herbaceous species (Wiegand, Saitz & Ward, 2006), which in turn attracts more grazers and the relatively high grazing intensity reduces fire-severity by reducing fuel load. Selective cutting may favour the dominance of drought-tolerant species (e.g. perennial grasses) while grazing and fire may reduce their abundance and the combined effect of these three factors eventually reduces the overall diversity of the herbaceous flora. Nonetheless, the effects of these disturbances are still highly variable depending on the type of plant community and the interactions with site specific ecological factors, such as soil and precipitation (Belsky, 1992; Harrison, Inouye & Safford, 2003). Like all

types of vegetation, the savannas reflect the interplay of changing sets of environmental conditions in space and time (Cole, 1982). Abiotic factors, such as climate and edaphic conditions, play a significant role in dictating vegetation structure and dynamics (Scholes & Walker, 1993). In savanna systems, abiotic variables (notably rainfall distribution, amount and intensity) have an overriding influence on vegetation dynamics (Wiegand, Saitz & Ward, 2006) due to the high variability between years. The interaction of disturbance regimes with other ecological factors reveals vegetation responses that are not apparent if the influence of fire, grazing, or selective cutting were studied individually (McNaughton, 1983). Interactions between plants, disturbance (e.g. by fire and herbivory), climate and soil type may influence vegetation density at differing spatial and temporal scales (Gillson, 2004). Climate has the potential to influence ecological communities through altered disturbance regimes. For example, increased herbaceous phytomass production is positively correlated with the amount of rainfall (Puyravaud, Menaut & Abbadie, 1995) which in turn results large quantities of standing dead fuel during the dry season and thus high combustibility and fire risk (Hennenberg *et al.*, 2006).

Relevance of disturbance studies in Burkina Faso

In Burkina Faso, as in many tropical countries, degradation of savanna-woodlands due to agricultural expansion, overgrazing, fire and wood cutting is a serious environmental concern (Fries & Heermans, 1992). Currently the area of natural forest in the country is approximately 7 million ha. The remaining dry forests and woodlands are being preserved through the establishment of “State forest” reserves (representing 26% of the total land area) for wood as well as biodiversity conservation. These reserves are not strictly protected against human impact and are being utilized both legally and illegally by local people. They are, therefore, subjected to multiple disturbances, such as grazing, fire and selective tree cutting. These disturbances lead to ecosystem degradation associated with the disruption of the fundamental environmental cycles such as the continuous circulation of water, carbon and other nutrients, and the decline in plants and animal populations (Corvalan, Hales & McMichael, 2005). Ecosystem degradation affects human well-being by diminishing the supply of ecosystem services. The challenge is to use these unavoidable disturbances as management tools. By controlling their use (timing, frequency and intensity) it may be possible to allow multiple uses of forest resources.

For centuries, livestock production in the savanna-woodlands of Burkina Faso has been one of the main sources of livelihood. It is the second biggest sector after agriculture with mainly cotton production, which supports both local communities and the national economy (MARA, 1996). Livestock production, especially under extensive systems, is based on the use of natural pastures. Grazing in “State forests” has been forbidden by local authorities for a long time (Bellefontaine, Gaston & Petrucci, 2000) in order to avoid the potentially deleterious impact of grazing on the “forest” ecosystem. At present the judicial regulation of livestock grazing in the “forest” is fluid because of the scarcity of natural pasture. Thus, the environmental policy in Burkina Faso (MEE, 1997) has shifted from simple

conservation to “management conservation” implying the inclusion of pastoral activities in the forest management policy. At present there is a scarcity of scientific data on the impact of pastoral activities on the savanna-woodland dynamics. Some of the main issues are pastoral carrying capacities, forage biomass production and the interaction between herbivory with various management activities such as fire and cutting.

Since 1986 the “forest” management prescription recommends selective tree cutting in the “State forests” by harvesting 50% of the merchantable standing volume on a 20-year rotation (Bellefontaine, Gaston & Petrucci, 2000). These prescriptions are not based on scientific evidence and information is urgently needed to make judicious management decisions that will ensure sustainable multiple use of the savanna-woodlands. The co-existence of woody and herbaceous plants in savanna ecosystems enhances the opportunity for multiple use management, i.e., synchronizing animal husbandry with wood and non-wood “forest” production and biodiversity conservation. Therefore, it is crucial to understand disturbance dynamics in order to forecast future changes and to balance ecosystem conservation and societal consumption needs. So far, most studies of the Sudanian savanna-woodlands have focused on woody components (Gignoux, Clobert & Menaut, 1997; Nygård, 2000; Sawadogo, Nygård & Pallo, 2002; Nygård, Sawadogo & Elfving, 2004; Zida *et al.*, 2007) and the herbaceous component has gained recently limited research attention (Sawadogo, Tiveau & Nygård, 2005). Papers in this thesis will, hopefully, contribute to filling the gaps in our knowledge of the dynamic responses of the herbaceous vegetation components to single and multiple disturbances.

Objectives

The general objective of the work presented in this thesis was to increase knowledge supporting multiple use management of the savanna-woodland in Burkina Faso. The studies presented in this thesis assess the impact of different disturbance regimes (fire, grazing, selective tree cutting and their interactions) on structural and functional attributes of the herbaceous vegetation community in the Sudanian savanna-woodland. The specific objectives were:

- (1) Assessing fire characteristics and temperature in relation to the dominant grass type, grazing and weather conditions (**Study-I**);
- (2) Examining long-term responses of species richness, abundance and diversity of the herbaceous vegetation to fire, grazing, selective tree cutting and their interactions (**Study -II**);
- (3) Analyzing the dynamic responses of herbaceous vegetation communities to disturbances using Principal Response Curves – a methodological consideration (**Study -III**);
- (4) Determining the effects of fire and grazing intensity on soil physico-

chemical and hydrological properties and aboveground biomass of the herbaceous vegetation (**Study-IV**);

- (5) Examining the effect of annual early fire on dry matter production and nutrient composition of selected grass species (**Study-V**).

The overall hypothesis of the studies was that disturbances by fire, herbivory and selective tree cutting affect the structural and functional components of savanna-woodland ecosystem; also that these disturbances effects are driven by stochastic environmental variability, such as rainfall, and could be used as a management tool provided an adequate level is found.

Material and Methods

Research sites

Studies **I**, **III** and **IV** were undertaken at Tiogo State forest (12°13' N, 2°42' W) while studies **II** and **V** were carried out at both Tiogo and Laba (11°40' N, 2°50' W) State forests (forêts classées). Both sites are located on flat areas at an altitude of 300 m above sea level in Burkina Faso, West Africa. The Laba and Tiogo State forests were delimited by the colonial French administration in 1936 and 1940 and cover 17 000 ha and 30 000 ha, respectively. Both forests are located along the only permanent river (the Mouhoun, formerly known as the Black Volta) in the country. Phyto-geographically, the experimental sites are situated within the Sudanian regional centre of endemism (White, 1983) in the transition from the north to south Sudanian Zone (Fontes & Guinko, 1995) (Fig. 2). The vegetation type at both sites is a tree and shrub savanna with a grass layer dominated by the annual grasses *Andropogon pseudapricus* Stapf. and *Loudetia togoensis* (Pilger) C.E. Hubbard as well as the perennial grasses *Andropogon gayanus* Kunth. (dominant in Tiogo) and *Andropogon ascinodis* C.B.Cl. (dominant in Laba). In the study area, these two perennial grasses are the most important species for fodder, construction (roof-thatching and fences) and handicrafts. The main forb species are *Cochlospermum planchonii* Hook. F., *Borreria stachydea* (DC.) Hutch. and Dalz., *Borreria radiata* DC. and *Wissadula amplissima* Linn. Species of the Mimosaceae and Combretaceae families dominate the woody vegetation component at both sites. In terms of basal area, the main woody species are *Detarium microcarpum* Guill. & Perr., *Combretum nigricans* Lepr. ex Guill. & Perr., *Acacia macrostachya* Reichenb. ex Benth., *Entada africana* Guill. & Perr., *Lannea acida* A. Rich., *Anogeissus leiocarpus* (DC.) Guill. & Perr. and *Vitellaria paradoxa* C.F. Gaertn. At Laba experimental site, at the beginning of the study period the mean basal area of woody species at stump level (20 cm) was 10.7 m² ha⁻¹ and 6.3 m² ha⁻¹ at breast height (130 cm), and the stand density was 582 individuals ha⁻¹ having at least one stem ≥10 cm GBH (girth at breast height). At Tiogo, the equivalent figures were 10.9 m² ha⁻¹ at stump level, 6.1 m² ha⁻¹ at breast height and 542 individuals ha⁻¹ (Sawadogo, Tiveau & Nygård, 2005).

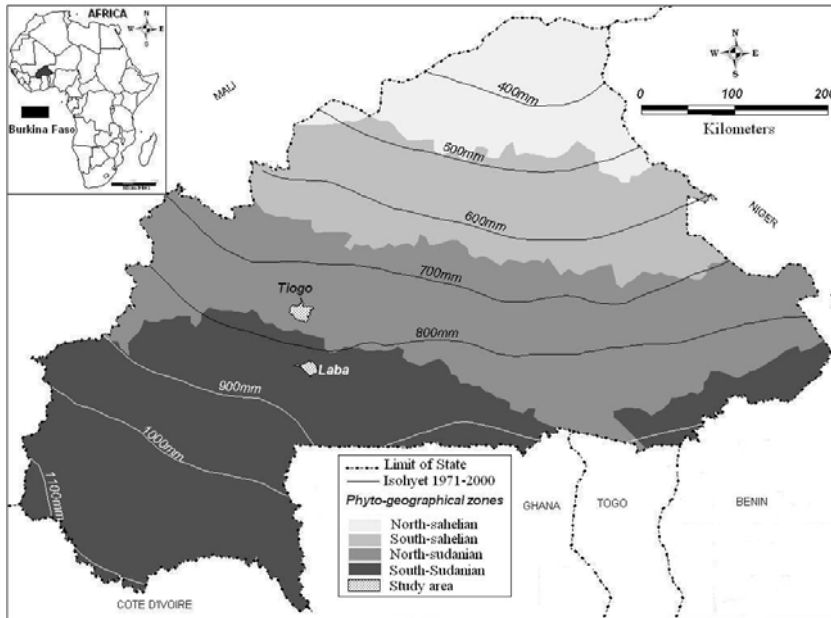


Fig. 2. Vegetation map of Burkina Faso with isohyets and location of the two study sites (Readapted April 2007 by CTIG/INERA/Burkina Faso after Fontes & Guinko 1995 and Direction of the National Meteorology).

The unimodal rainy season lasts for about 6 months, from May to October. The rainfall in the region is characterized by irregularity in rain efficiency both temporally and spatially. The mean (\pm SD) annual rainfall during the period (1992-2006) was 861 ± 143 mm at Laba and 847 ± 177 mm at Tiogo, and the number of rainy days per annum was 68 ± 17 and 67 ± 16 at Laba and Tiogo, respectively (Fig. 3). Characteristically, periods of one or more relatively wet years alternate with drier periods. Because of desiccating factors (temperature, low humidity, and dry winds) the effective precipitation is often far less than the average total rainfall would suggest. Mean daily minimum and maximum temperatures are 16°C and 32°C in January (the coldest month) and 26°C and 40°C in April (the hottest month), yielding an aridity index (Brown & Lugo, 1982) of 3.5 and 3.7 for Laba and Tiogo, respectively. Wind speed varies depending on the period of the year and the time of day. Low wind speeds are usual from late in the afternoon (4 p.m.) until 7 a.m. on the following morning.

The most frequently encountered soils are Lixisols (Driessen, Deckers & Spaargaren, 2001); the soil at Laba is shallow (< 45 cm depth) silty-sand and at Tiogo it is mainly deep (>75 cm) silty-clay. These soils are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo, 1998). The main soil properties at the experimental sites were: Clay ($24.8 \pm 7.7\%$), fine silt ($15.0 \pm 4.3\%$), coarse silt ($25.4 \pm 3.0\%$), fine sand ($21.7 \pm 6.7\%$), coarse sand ($13.1 \pm 4.2\%$), total organic matter ($1.8 \pm 0.7\%$), total N ($0.1 \pm 0.0\%$), C/N ($11.4 \pm 4.6\%$), available P (1.4 ± 0.7 ppm), pH H_2O (6.2 ± 0.5) at Tiogo. The corresponding values at Laba were: Clay ($17.5 \pm 8.8\%$), fine silt ($8.7 \pm 2.4\%$), coarse silt ($16.4 \pm$

6.2%), fine sand ($16.7 \pm 4.3\%$), coarse sand ($40.0 \pm 11.6\%$), total organic matter ($2.1 \pm 0.6\%$), total N ($0.1 \pm 0.0\%$), C/N ($15.9 \pm 4.9\%$), available P (1.3 ± 1.0 ppm), pH H₂O (6.2 ± 0.7).

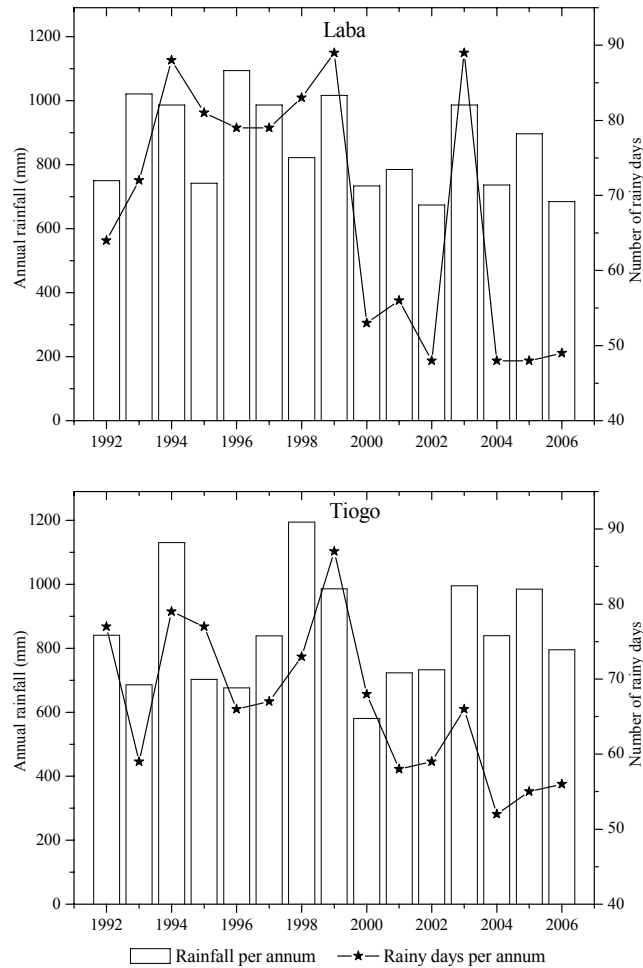


Fig. 3. Annual rainfall and number of rainy days for Tiogo and Laba across the study period.

Prior to the establishment of the experiment, the area was frequently grazed by livestock and wild animals and burnt almost every year, often late in the dry season (November to May). The livestock is dominated by cattle, although sheep and goats also graze these sites. The presence of livestock in the two state forests varies spatially and temporally (Savadogo, 2002), occurring mainly during the rainy season (June to October) when the grass is green and the surrounding areas are cultivated. During the dry season, when the crops are harvested, the cattle

mostly frequent the agricultural fields and at this time of the year the animals come to the forest mostly in search of water along the river. They then graze on straws in the bush clumps that have escaped the fire along with the young shoots of perennial grass species and young woody foliage induced by the fire. The livestock carrying capacity for Laba State forest has been estimated to be 1.0 Tropical Livestock Unit per ha (T.L.U. ha⁻¹) and 1.4 T.L.U. ha⁻¹ for Tiogo (Sawadogo, 1996). The grazing pressure at both experimental sites was about half of this capacity. The mean herbaceous biomass production for the period 1993-2001 was 3.47 ± 1.37 t DMha⁻¹ at Laba site and 4.01 ± 1.51 t DM ha⁻¹ at Tiogo (Sawadogo, Tiveau & Nygård, 2005). In both forests, trees are mainly cut for commercial fuelwood and poles by local populations that are organized in co-operatives. Non-timber forest products such as fruit, leaves, tubers, perennial grass straw and hay are also harvested in these state forests.

Methods

Study-I

In this study, fuel characteristics, fire behaviour and temperature were examined in relation to grazing, dominant grass type (annual or perennial) and wind direction (head fire or back fire) by lighting 32 early fires at Tiogo site. Burnt areas (20 × 20 m) were located on flat ground to eliminate the influence of slope on fire behaviour. Fire was ignited early in the morning or late in the afternoon with a drip torch to rapidly establish a fire line and to ensure linear ignition. Fuel characteristics were described based on the following variables: fuel load and composition, moisture content of the fuel, vegetation height, and cover estimated using the point intercept sampling procedure (Levy & Madden, 1933). Fuel characteristics were assessed at two occasions, pre- and post-burning in order to compute fuel consumption. To assess fuel loads, six quadrats of 1 × 1 m in each burnt area were established; these were sub-divided into four equal parts. Fuel was collected in two sections, on one diagonal, of each quadrat shortly before burning to determine the pre-burn fuel load, while fuel in the other two sections was collected after the fire was extinguished to determine the post-burn fuel load. Both the pre- and post-burning fuel were separated into litter (defined as dead and fallen tree and grass leaves), live fuel (green standing grass and herbs) and dead fuel (dead standing grass and stems), and immediately weighed. Moisture content of each fuel category was determined on a dry weight basis after oven-drying at 80°C until constant weight. Fire behaviour parameters (fuel consumption, rate of spread, fire intensity, and flame height) were assessed. The fuel consumption was calculated as the difference between the pre and post fire fuel loads. The rate of spread was determined by recording the time the fire front took to reach pre-placed poles, 5 m apart, on either side of the burning plot. Fire intensity was estimated using the equation developed by Byram (1959). Flame height of the moving fires was measured vertically from the ground. Fire temperatures were recorded using MiniCube data loggers with 10 thermo elements type-K (Model VC, Environmental Measuring Systems, BRNO, Czech Republic) and probes

placed at -10, -5, -2, 0, 20, 50, 150, 300, 500 cm. For each fire, the maximum temperature at each probe position was used for data analysis. The series of temperature measurements at each probe position was also used to calculate the temperature residence time above 60°C, the threshold considered lethal for plant tissues (Daniell, Chappell & Couch, 1969). Weather data (open wind speed, air temperature and relative humidity) during burnings were recorded every minute using an in situ automatic weather station placed at 1.8 m. These data were used while developing fire behaviour prediction models.

Study-II

This study dealt with the effects of grazing, fire and selective tree cutting on species richness, abundance and diversity of herbaceous vegetation at both Tiogo and Laba. A factorial experiment was established in each of the two State forests (Fig. 4). Each experimental site (18 ha) was divided into two main plots; one was fenced to exclude livestock and the other was open to grazing. Each main plot was further divided into 4 blocks of 2.25 ha, each containing four plots of 0.25 ha (50 by 50 m). The plots were separated from each other by 20-30 m fire-breaks. To the four plots, the following factorial treatment combinations were randomly assigned; no cutting – no fire, no cutting – early fire, cutting – no fire, and cutting – early fire. The selective cutting treatment was applied once at the beginning of the experiment (1994) by removing 50% of the merchantable standing volume of trees at stump level. The selective cutting was undertaken in December 1993 at Tiogo and a month later in January 1994 at Laba. Prior to cutting, all species were categorized according to their local uses as: protected species, timber, poles and fuelwood, and fuelwood and other uses (Hagberg, Gomgnimbou & Somé, 1996; Sawadogo, 1996). Individuals of other categories except protected species were cut according to the following size criteria: > 30 cm butt diameter for timber species, > 14 cm diameter at stump level for poles and fuelwood species and > 8 cm diameter at stump level for fuelwood and others uses (Sawadogo, Nygård & Pallo, 2002). The early fire was applied at the end of the rainy season (October-November) each year since the establishment of the trials when the grass layer humidity was approximately 40%.

The point-intercept sampling procedure (Levy & Madden, 1933) was used to gather species-cover data annually at the end of the rainy season (September to October) when most of the species are flowering and fruiting, thus facilitating species identification. The presence of species was recorded along a 20 m permanent line laid in each plot. At every 0.20 m a pin of 6 mm diameter, taller than the maximum height of the vegetation was lowered from above; and a species was considered as present if the pin hit any of its live parts. Identification of species and families of plants followed Hutchinson *et al.* (1954). Abundance, species richness and diversity were computed for each replicate in each treatment, for each life form (annual grasses, perennial grasses and forbs) and for some selected species (*Andropogon ascinodis* and *Diheteropogon hagerupii* at Laba and *Andropogon gayanus* and *Loudetia togoensis* at Tiogo).

Abundance was expressed as percentage cover and species richness as total number of species. Species diversity (H') was calculated using the equation given below:

$$H' = -\sum p_i \ln p_i$$

where p_i is the relative abundance of species i in a plot (Magurran, 2004).

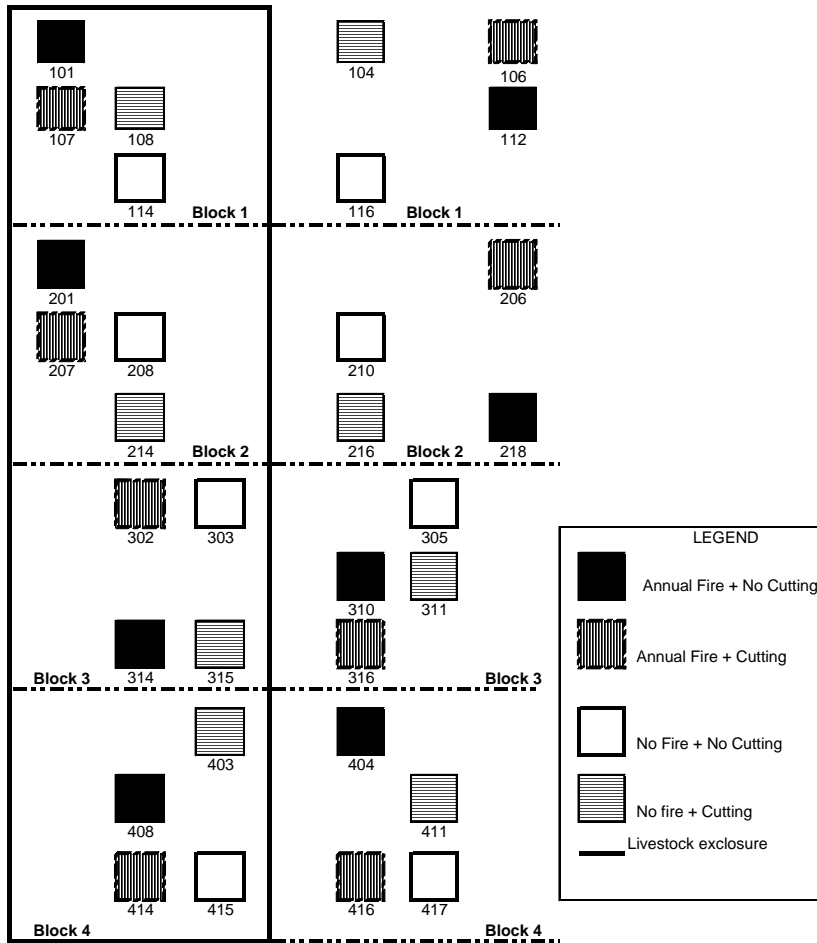


Fig. 4. Lay-out of the factorial experimental design employed.

Study-III

The main focus of this study was the application of the Principal Response Curves method for analyzing the response of herbaceous vegetation communities to disturbance regimes (fire, grazing and selective cutting) over time. PRC analysis is an ordination method based on partial redundancy analysis. It is used for the analysis of community response data from designed experiments sampled repeatedly through time (van den Brink & ter Braak, 1998; ter Braak & Smilauer, 2002). Associated with each PRC is a set of species weights, which reflect the influence of particular species on the overall community response described by the PRC scores over time. The species abundance data from Study-II were used for this analysis.

Study-IV

The effects of grazing intensity at four levels (light grazing, moderate grazing, heavy grazing and very heavy grazing) and fire at two levels (early burning or long-term fire protection) on above ground phytomass and soil properties were investigated in this study. The percentage cover of herbaceous vegetation, biomass and litter were determined using the intercept sampling procedure (Levy & Madden, 1933) and hand clipping of representative 1 m² quadrats. The soil compaction effect of livestock grazing was determined by measuring water infiltration rate using double ring infiltrometers (Bouwer, 1986). For analyses of soil chemical properties, composite soil samples were taken at a depth of 0-10 cm and analyzed for the total N using Kjeldahl procedure, organic matter was determined according to Walkley and Black (1934), available K, Ca and Mg by atomic absorption spectrometry and available P using a Bray-1 extract (Olesen & Dean, 1965). Soil physical properties were also determined following standard procedures.

Study-V

The effects of annual early fire on dry matter production and the cumulative fire effect on nutrient composition of four ecologically and socio-economically valuable grass species, *Andropogon gayanus* Kunth, *Diheteropogon amplexans* W. D. Clayton, *Chasmopodium caudatum* Stapf., and *Rottboellia exaltata* Linn., were investigated in this study. These species are commonly used for feeding livestock in the study area. Eight plots (4 burnt and 4 unburnt) from the non-grazed area at Tiogo site were selected, and six 1 × 1 m quadrats were marked for annual sampling of herbaceous biomass during the study period (1993-2004). The location of these quadrats was chosen systematically to avoid selecting the same location in consecutive years. Plants were harvested manually by cutting at the base (approximately 10 cm above ground) each year at the end of the rainy season (mid October). The samples were then bagged, air-dried until constant mass, and weighed to determine their dry matter. For each species, two composite samples were taken from burnt and unburnt plots in 2004. The plant samples (whole plant including stems, leaves, flowers and capsules) were dried in a forced draught oven at 60 °C and the samples were ground to pass through a 1.0 mm screen using a Christy & Norris Laboratory Mill. Samples were analyzed for crude protein (CP),

neutral detergent fibre (NDF), acid detergent fibre (ADF), crude fat (CF), non structural carbohydrates (starch + sugars), neutral detergent insoluble crude protein (NDICP), neutral detergent fibre digestibility (NDFD), and In Vitro True Digestibility (IVTD) following standard procedures. The total mineral content (ash) and the concentrations of macro-mineral elements (Ca, P, Mg, K, Na) and the trace elements (Fe, Zn, Cu, Mn, Mo) were also analyzed using standard procedures (Sirois *et al.*, 1994). As measures of digestibility and metabolizable energy, Total Digestible Nutrients (TDN), Net Energy for Maintenance (NEM), Net Energy for Lactation (NEL), relative feed value (RFV), and relative forage quality (RFQ) were estimated. All analyses were performed in a commercial laboratory in the USA (Dairy One, Ithaca, NY, USA) specializing in Cornell net carbohydrate and protein systems (Sniffen *et al.*, 1992).

Data analysis

Collated data in these studies were subjected to analysis of variance (ANOVA) using the SPSS software package (Copyright SPSS for Windows, Releases 2004 and 2005 Chicago: SPSS Inc.). The general linear model (GLM) univariate (**I**, **III**, **IV**) or repeated measures (**II**) was chosen as deemed applicable. Data were checked for normality before analysis. Means that showed significant differences at $p < 0.05$ were compared using Tukey's pair-wise comparison procedures. Correlation analyses were performed to detect relationships between variables. Fire behaviour prediction models were derived from stepwise multiple regressions (backward elimination with 5% significance level). For the analysis of the herbaceous vegetation community response to disturbance regimes, Principal Response Curves (PRC) analysis were performed (van den Brink & ter Braak, 1998) using the software package CANOCO 4.5 (ter Braak & Smilauer, 2002).

Results and Discussion

Assessment of disturbance – fire characteristics

Fuel and fire characteristics and temperature were studied in relation to grazing, dominant grass type and wind direction. The results (Table 2) demonstrated that grazing significantly reduced the vegetation height, total fuel load, and dead and live fuel fractions. Plots dominated by perennial grasses had higher values for vegetation height, total fuel load, and the quantity and moisture content of the live fuel load. This effect is related to herbage removal and trampling pressure (static load) exerted by the animals, which are the best known grazing disturbance factors that affect vegetation structure (Frost *et al.*, 1986; Rietkerk *et al.*, 2000). The effect of grazing on fuel load also interacts with vegetation type. In the vegetation dominated by annual grasses (*Loudetia togoensis* and *Andropogon pseudapricus*), the quantity of litter fuel was higher on non-grazed ($0.56 \pm 0.05 \text{ kg m}^{-2}$) than grazed areas ($0.34 \pm 0.03 \text{ kg m}^{-2}$). The effect of grazing was not significant on vegetation dominated by perennial grasses (*Andropogon gayanus* and *Diheteropogon amplexans*). The fact that moderate grazing reduces annual grass

fuel load suggests that this grazing system could be advantageous in reducing the severity of fire, as evidenced by the significantly lower fuel consumption by fire on grazed compared with non-grazed areas (Table 2).

Despite significant effects on total fuel load, both grazing treatment and vegetation type did not affect the rate of spread and fire intensity ($p > 0.05$). The free grazing strategies of mixed herds (cattle, sheep and goats) adopted in the experiment creates spatial differences in terms of grazing intensity, stocking rate and feeding behaviour that in turn might not sufficiently decrease the horizontal and vertical fuel continuity. The rate of spread of fire was faster during head than back fire and flame length was shorter in head fire than back fire (Table 2). In head fire, intensity and rate of spread were also closely related to wind speed ($r^2 = 0.82$ and 0.72 for fire intensity and rate of spread, respectively). Apparently both wind direction and speed have a strong effect on fire behaviour in the Sudanian savanna-woodland, as documented previously in other vegetation communities (Cheney, Gould & Catchpole, 1993; Trollope, Trollope & Hartnett, 2002; Bilgili & Saglam, 2003). The effect of wind speed is attributed to enhanced supply of oxygen to the fire (Trollope, de Ronde & Geldenhuys, 2004), which stimulates the heat transfer by conduction or radiation which in turn results in preheating of the fuel ahead of a fire front. Wind direction and speed also affected rate of spread because they can be responsible for tilting the flames towards the fuel ahead of the fire. In general, increased wind speed results in an exponential increase in the rate of spread during head fire compared with back fire (e.g. Govender, Trollope & Van Wilgen, 2006). The ranges of fire behaviour variables found in the present study were comparable to those reported from the savanna-woodland ecosystems in southern Africa (Shea *et al.*, 1996; Gambiza *et al.*, 2005). The rate of spread and fire intensity were negatively correlated with relative air humidity ($r^2 = -0.62$ and -0.72 , respectively). Since high relative humidity results in increased moisture content of fuel, the amount of heat necessary to reach the point of ignition will increase, thereby leading to reduced combustibility. Fire behaviour parameters during head and back fire were not significantly correlated with ambient air temperature, probably because of the narrow range of air temperatures during the experimental burning.

The average maximum temperature was high in the non-grazed plots where annual grasses dominate, and on plots subjected to head fire (Table 2). Livestock grazing significantly reduced fire temperature and residence time of temperature above 60°C ; this is because it removes biomass and creates patchiness in the fuel bed. Plots dominated by annual grasses were hotter than those dominated by perennial grasses; this can be explained by the level of desiccation during prescribed burning. The moisture content of live fuel in the plots dominated by perennial grass was substantially higher than those in plots dominated by annual grass. The overall temperature was higher in head fire than in back fire, however at the surface (0 cm) the majority of back fires were hotter than the head fires. This is consistent with findings by Trollope *et al.* (2002). Fire temperature and residence time also varied significantly with respect to probe location (Fig. 5). The highest values were recorded at the soil surface (0 cm). Generally fire temperatures and residence times were higher above the soil surface than below it, with a tendency to decrease with increasing soil depth.

Table 2. Main effects of grazing, vegetation type and wind direction on total fuel load, fire behaviour parameters (mean \pm standard error), maximum fire temperature ($^{\circ}$ C \pm standard error) and residence time (minutes \pm standard error) of temperature above 60 $^{\circ}$ C.

	Grazing treatment		Vegetation type			Wind direction	
	Grazing	No grazing	Annual	Perennial	Head Fire	Back Fire	
Total fuel load (kg m ⁻²)	0.42 \pm 0.03*	0.73 \pm 0.07	0.45 \pm 0.04*	0.70 \pm 0.07			
Dead fuel load (kg m ⁻²)	0.14 \pm 0.02*	0.24 \pm 0.02	0.21 \pm 0.02	0.17 \pm 0.03			
Live fuel load (kg m ⁻²)	0.09 \pm 0.03*	0.25 \pm 0.08	0.00 \pm 0.00*	0.34 \pm 0.06			
Vegetation height (cm)	122.71 \pm 16.25*	170.21 \pm 21.21	84.58 \pm 4.28*	208.33 \pm 16.14			
w (kg m ⁻²)	0.33 \pm 0.04*	0.50 \pm 0.05	0.42 \pm 0.038	0.41 \pm 0.06	0.42 \pm 0.05	0.41 \pm 0.04	
FH (cm)	150.91 \pm 23.68	135.78 \pm 21.27	160.99 \pm 21.49	125.70 \pm 22.75	177.47 \pm 24.10	109.22 \pm 16.88*	
r (m s ⁻¹)	0.08 \pm 0.03	0.04 \pm 0.01	0.08 \pm 0.03	0.05 \pm 0.02	0.11 \pm 0.03	0.02 \pm 0.00*	
I (Kj m ⁻¹ s ⁻¹)	1508.60 \pm 799.28	504.37 \pm 276.99	1165.06 \pm 476.16	847.91 \pm 720.49	1831.26 \pm 810.00	181.71 \pm 48.88	
Temperature	126.57 \pm 12.74*	200.16 \pm 15.54	189.53 \pm 16.38*	137.21 \pm 12.03	174.65 \pm 14.74	152.08 \pm 14.26	
Residence time	0.72 \pm 0.11*	1.02 \pm 0.10	0.88 \pm 0.09	0.86 \pm 0.12	0.77 \pm 0.10*	0.97 \pm 0.11	

w: fuel consumption; FH: Flame height (cm); r: rate of spread; I: Fire intensity; * significant, p < 0.05

Our results are in agreement with previous reports. For example, Bradstock and Auld (1995) reported soil temperatures above 60°C in the top three centimetres during burns in Australian bush lands; Miranda (1993) reported a temperature of 55°C at 1 cm depth during a Cerrado fire in Central Brazil; Auld and O’Connell (1991) found temperatures of above 80°C in the top 2 cm for fires of medium intensity; and Silva *et al.* (1990) reported temperatures of 101°C in the upper 5 mm of soil in the savanna in Western Venezuela. It is generally believed that fire temperature decreases with increasing soil depth in a negatively exponential manner (De Luis *et al.*, 2004); this is related to the thermal conductivity across the soil profile (Valette *et al.*, 1994). Differences in fire temperature reported in the literature might be due to differences in chemical and physical (dead fuel fraction, and compactness of the fuel bed) properties of the fuel along with weather conditions during burning and the heat capacity and thermal conductivity of the soil. Fire temperatures at the surface and at different vertical positions have an important effect on the structure of the herbaceous vegetation community via recruitment and establishment of seedlings. Since seeds of most savanna-woodland species have inbuilt physical dormancy (Baskin & Baskin, 1998), the high temperature at the surface could stimulate germination while that above the soil surface could induce seedling shoot die back (Hoffmann & Solbrig, 2003), thereby making the transition time from seedling to sapling longer if frequent fire occurs. Since the temperature at 10 cm below the surface is low (35°C), plant root systems are likely to be safe from heat shock.

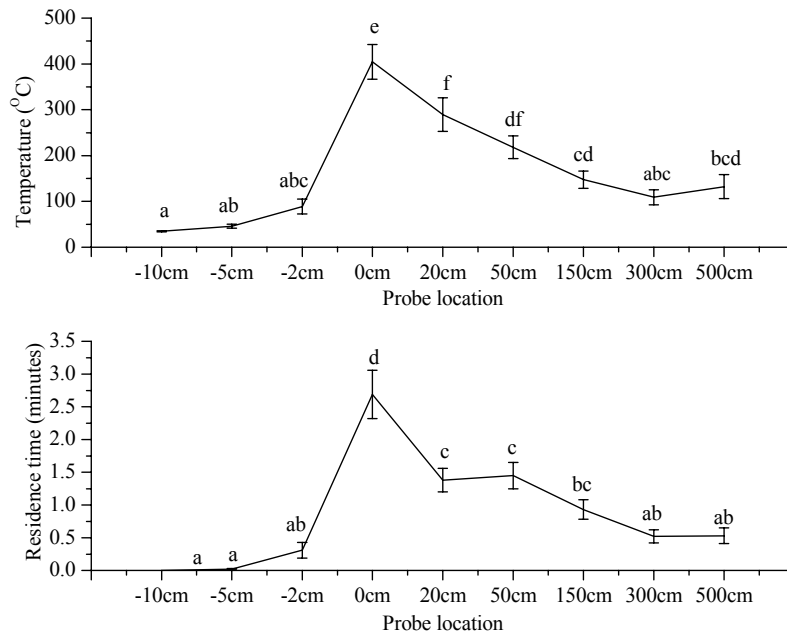


Fig. 5. Main effects of probe location on maximum fire temperature ($^{\circ}\text{C} \pm$ standard error) and residence time (minutes \pm standard error) of temperature above 60°C. Means with different letters are significantly different based on Tukey’s HSD test.

The fire behaviour prediction models (Table 3) show that wind speed and total fuel load explained 56% and 73% of the variations in rate of spread and fire intensity, respectively, during head fire. The total fuel load alone explained 86% of the variation in fuel consumption during head fire. Fire intensity and the rate of spread during back fire could be predicted using wind speed, vegetation cover and height, which respectively explained 81% and 63% of the variations in fire intensity and rate of spread. The total fuel load described 71% of the variation in fuel consumption during back fire. Since the models are statistically significant and conceptually meaningful and logical, they can serve as a guide for predicting fire behaviour in the study area. It should, however, be noted that some of the correlation and regression results seemed inconsistent, for example total fuel load and fuel consumption during burning were positively correlated while the rate of spread and total fuel load did not; so also the negative relationship between fire intensity and total fuel load. This is indeed not surprising because the fire intensity and its rate of spread are influenced by the moisture conditions and temperature of fuels at the time of fire occurrence as the rate of combustion of moist, cold fuels is slower than that of dry, hot fuels (DeBano, Daniel & Peter, 1998). This is further supported by the large quantity of live perennial fuel load with high moisture content observed during prescribed early fire in our study. As a whole, the predictor variables can be measured relatively easily on site thus making these models practically useful for monitoring annual fire. Although very little work has been done on predicting fire behaviour in West African savanna ecosystem, our result is comparable to studies made in other savanna or grass land ecosystems (e.g. Trollope, Trollope & Hartnett, 2002).

Table 3. Regression equations for predicting rate of fire spread (r), fuel consumption (w) and fire intensity (I) in savanna-woodland. The predictors were wind speed (W), total fuel load (TFL), vegetation cover (VC), vegetation height (Ht). SEE = standard error of estimation

	Variable	SEE	r^2	p
Head Fire	$r = 0.1042 + 0.1301W - 0.1418 TFL$	0.0879	0.557	0.005
	$w = 0.0877 + 0.7006 TFL$	0.0600	0.862	<0.0001
	$\text{Log}(I) = 1.84 + 1.81W - 1.22TFL$	0.8148	0.731	<0.0001
Back Fire	$r = 0.045 + 2310^{-4}W + 210^{-4}VC - 910^{-5}Ht$	0.0062	0.631	0.006
	$w = 0.1294 + 0.6436 TFL$	0.0652	0.705	<0.0001
	$\text{Log}(I) = 1.52 + 1.40W - 4110^{-4}Ht + 3710^{-5}VC$	0.4756	0.807	<0.0001

Structural responses to disturbances

Long-term effects of multiple disturbances and their interactions on herbaceous vegetation at both Tiogo and Laba were analyzed. The results show that grazing had no effect ($p > 0.05$) on total species richness, diversity and abundance of

herbaceous vegetation at either study site (Fig. 6). There are three possible reasons why grazing had no impact on these measures. First, the grazing intensity on our plots was half the carrying capacity, thus many species could survive intermediate levels of grazing, which allows succession to proceed but limit the ability of few highly competitive species to dominate the community (Olf & Ritchie, 1998). Second, the experimental sites have been subjected to various disturbances, such as bush fire and grazing by domestic and wild animals for many years prior to the establishment of the experiment, thus the herbaceous species might be evolved in association with herbivory. Third, the effect of year \times grazing interaction was significant for total species richness ($p < 0.001$), abundance ($p = 0.021$) and richness of annual grasses ($p = 0.003$) and forbs ($p = 0.014$) at Tiogo; i.e. higher on grazed than non-grazed plots over the study period, suggesting spatial and temporal variations in terms of grazing intensity, stocking rate and feeding behaviour, which could average out the overall effect of grazing.

Grazing, however, reduced ($p = 0.051$) the abundance of herbaceous flora, particularly perennial grasses ($12.0 \pm 5.5\%$ and $16.7 \pm 3.5\%$, respectively for grazed and non-grazed plots) at Laba. This could be related to trampling effect, which in turn is related to the species ability to resist trampling-induced changes, their tolerance to a cycle of disturbance and their resilience following post trampling (Cole, 1995). Some species, namely *Borreria stachydea*, *Zornia glochidiata* and *Pandiaka heudelotii*, were found solely in grazed plots during 1998 assessment that were not recorded earlier on the same plots. Herbivores play an important role in seed dispersal, germination, soil seed bank composition and localized fertilization effects of dung and urine (O'Connor & Pickett, 1992; Haurault & Hiernaux, 2004), thereby enabling species to colonize grazed sites. The new species that appeared on grazed plots in our study sites have previously been described as indicators of grazing disturbance in the Sudanian savanna (Cesar, 1992).

The main effects of repeated early fire on total species richness, abundance and diversity were not significant at either of the study sites, but fire had a positive effect ($p = 0.048$) on species richness of annual at Tiogo and opposite effect on abundance of perennial grasses at Laba (Fig. 7), which is consistent with previous study in the Serengeti grasslands (Belsky, 1992). Inhibition of emergence and establishment of herbaceous species in savannas is related to high fire intensity (Jensen, Michelsen & Gashaw, 2001) that results in increased seed mortality, and an inverse relationship has been observed between fire severity and species richness (Jensen & Friis, 2001). However, early fire is often of low intensity and severity due to high moisture in the fuels and thus has minor impact on seed viability while creating conditions favourable for germination and favouring tillering by removal of litter cover (Whelan, 1995; Garnier & Dajoz, 2001). Germination of several herbaceous species is also stimulated by smoke released during burning (Clarke, Davison & Fulloon, 2000; Adkins & Peters, 2001). The effect of fire on species richness and diversity of annual grasses showed a significant temporal variation, especially at Tiogo site.

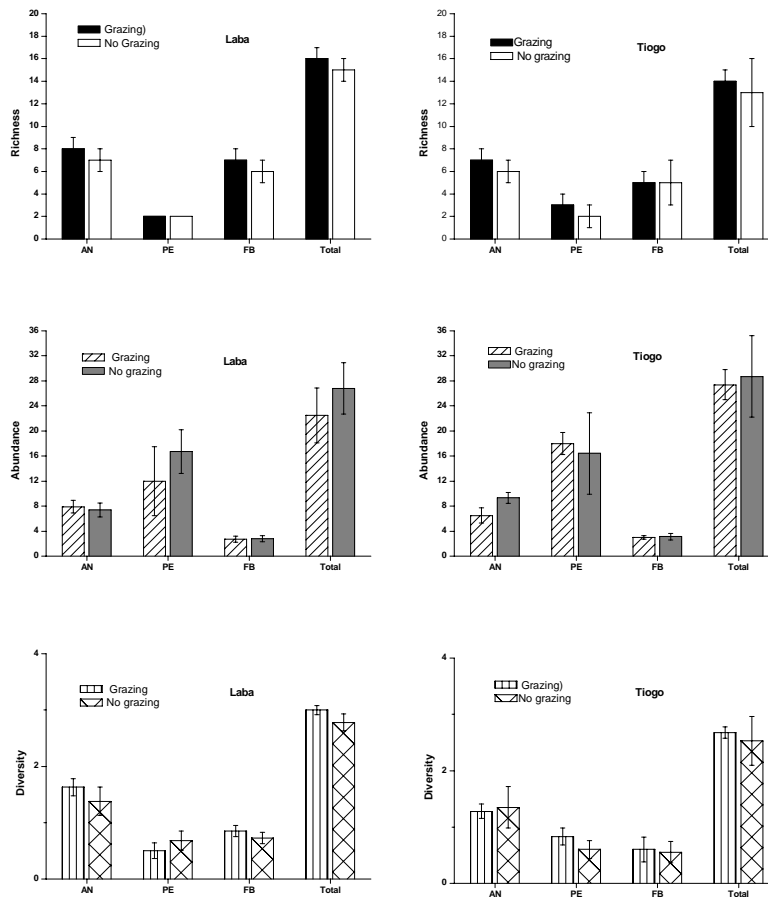


Fig. 6. The main effects of grazing on species richness, abundance and diversity of herbaceous vegetation in the Sudanian savanna-woodlands at Laba and Tiogo (AN: annual grasses, PE: perennial grasses, FB: forbs).

For example the richness of annual grasses was two times higher on burnt than unburnt plots after three (1996) and nine (2002) years while diversity of annual grasses was nearly tripled after two (1995), four (1997) and five (1998) years compared to the control plots. This could be related to inter-annual variation in fire intensity and severity, which in turn depends on the life form, quantity of fuels, weather conditions and moisture content of fuels (Coughenour, 1991; Cheney, Gould & Catchpole, 1993), and the ability of some grasses to fully recover after fire, which may require 2 to 4 years or more (Bock & Bock, 1992). The relatively large number of species found on burnt plots in our study is consistent with previous studies on arid plant communities (Valone & Kelt, 1999; Valone, 2003). At Laba, fire significantly reduced the abundance of perennial grasses (Fig. 7). Perhaps, the intensity of fire could be sufficiently high at plots level to the extent of hampering the resprouting of some perennial grass from

buried vegetative structures. Uniform burn is difficult to achieve in savanna-woodlands due to their mosaic architecture with bush clumps and open areas, so fire generally skirts around the edges of bush clumps, leaving the centre unburnt.

Selective removal of trees is thought to enhance the colonization process by reducing competition for water and nutrients, opening up more growing space and by increasing the availability of light at the ground level (Frost *et al.*, 1986). Our results show that total species richness, abundance and diversity tended to be higher during the first 2-3 years after selective cutting and fluctuate thereafter.

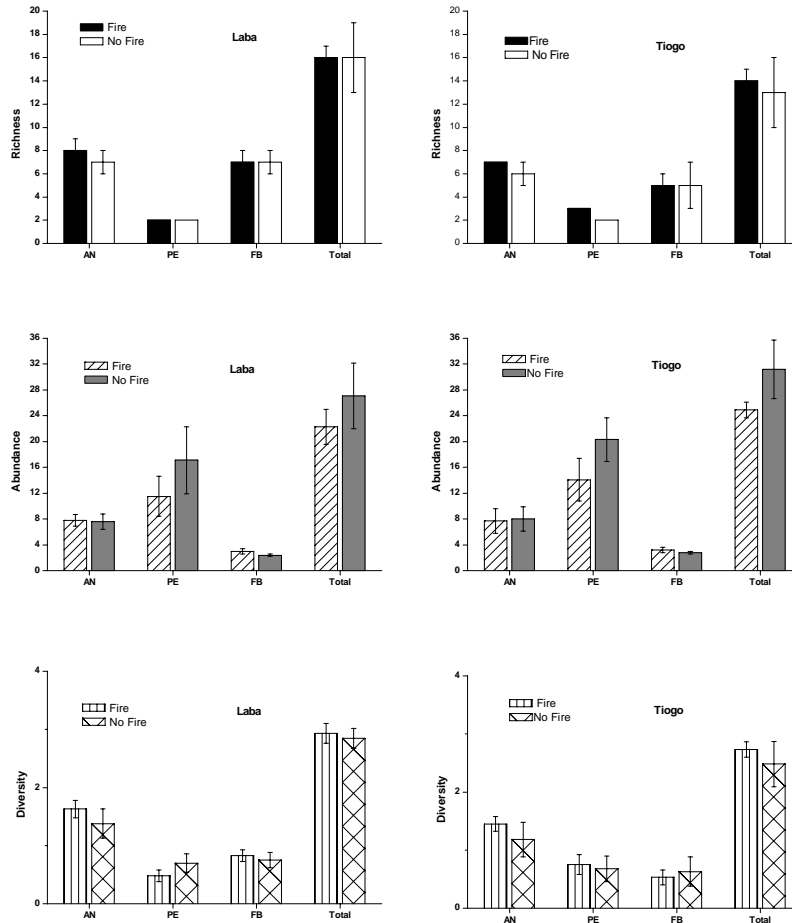


Fig. 7. The main effects of fire on species richness, abundance and diversity of herbaceous species in the Sudanian savanna-woodlands at Laba and Tiogo (AN: annual grasses, PE: perennial grasses, FB: forbs).

Selective cutting however had no effect ($p > 0.05$) either on species richness, abundance and diversity of different life forms. The selective cutting treatment was applied once by extracting 50% of the basal area of all trees; therefore, the

competition for light, water and nutrients might have been determined by initial density of trees. For instance, if tree density was high before cutting, selective cutting of trees might reduce the competition for resources and thus have a clear effect. However, the woody component of most savanna-woodlands are scattered and further opening of the canopy can create unfavourable thermal condition in the understory that increases soil evaporation and plant evapotranspiration, thereby counterbalancing the initial positive effect of increased water and nutrient availability due to selective removal of trees. There is also evidence from the same sites (Sawadogo, Nygård & Pallo, 2002; Nygård, Sawadogo & Elfving, 2004) that shows vigorous resprouting and suckering ability of most savanna woody species following cutting disturbance. Since the sprouts and suckers depend on the already established root system of the original tree for accessing water and soil nutrients, they can easily out-compete the herbaceous vegetation.

There is insufficient evidence to suggest that combining annual early fire, grazing and selective tree cutting always affects herbaceous species richness, abundance and diversity in the Sudanian savanna-woodland. The limited interactions effects were life form and site specific. At all levels of grazing at Laba, the richness of herbaceous flora was slightly lower on plots subjected to fire × cutting treatment than plots subjected to either fire or cutting treatments while the reverse held true for total abundance ($p < 0.05$). At life form level, fire × grazing treatment significantly reduced the species richness of forbs at Tiogo ($p = 0.029$) compared to grazing treatment alone while fire × grazing treatment resulted in significantly higher forbs diversity ($p = 0.029$) than either grazing or fire. The diversity of forbs was also significantly influenced by the interaction of the three factors at Tiogo ($p = 0.036$). Forb diversity was higher on plots subjected to fire × grazing × cutting than on plots subjected to neither of these treatments. These results contrast with earlier reports in mesic grasslands where grazing and burning interact to increase plant species richness and diversity to unusually higher level (Collins & Barber, 1985; Collins, 1987). In mesic grasslands, burning opens space for colonists and grazing limits the ability of competitively dominant C_4 grass species to out-compete other plants, resulting in opportunities for colonization by C_3 grasses and forbs (Collins, 1987; Collins *et al.*, 1998). In semi-arid savannas, plant communities tend to have less ground cover and presumably less competition for space (Valone & Kelt, 1999). The limited interaction effects of grazing and fire have been observed in other arid plant communities (Belsky, 1992; Valone & Kelt, 1999; Drewa & Havstad, 2001; Valone, 2003). The additive effects of fire and grazing could have resulted from different sets of species responding positively or negatively to each disturbance or from the fact that fire simply duplicated the effect of grazing by reducing above ground biomass. The current level of herbivory might be insufficient to negatively affect species. Therefore interpretations of the results are limited to the moderate level of grazing in the present study.

The vegetation dynamics cannot be solely attributed to fire, grazing or tree canopy but partly explained by short and long-term fluctuations of other ecological factors, such as soil fertility and precipitation. The site-specific nature of this relationship could very well depend on the soil characteristics. The soils at Laba are shallow (< 45 cm depth) and silty-sand in texture while the soils at Tiogo

are silty-clay and mainly deep (>75 cm). The deeper soils at Tiogo are more favourable for the high biomass production of perennial grasses like *Andropogon gayanus* and *Diheteropogon amplexans* (Sawadogo, Tiveau & Nygård, 2005). These two species also greatly contributed to the high abundance found at this site. The inter-annual variation in total species richness, abundance and diversity were poorly related to the amount and frequency of rainfall at Laba ($r^2 < 0.24$ in all cases). At Tiogo, more than 50% of the inter-annual variation in abundance and diversity of herbaceous species was attributed to rainfall. Herbaceous response to rainfall varied among growth forms and correlation coefficients increased slightly in multiple factors than the analysis of precipitation or rainy days alone. We observed that early heavy rains stimulated seed germination within three days (personal observation) but frequent gaps in rainfall distribution caused wilting of emerging seedlings; another field observation was that the topsoil layer dries out very quickly after first rain event because of wind and of direct insolation. This observation is supported by the findings of Seghieri *et al.* (1994) who under similar climatic conditions found that the species composition was strongly dependent of intra seasonal drought stress, especially at the beginning of the rainy season. In the semi-arid rangelands, the first small showers at the end of the dry season stimulate seeds of fast-germinating species, but slower germinating species need several rains (Elberse & Breman, 1990); dry spells following the first rains favour slow germinating species.

Community Responses to disturbance dynamics

The multivariate ordination technique Principal Response Curves (PRC), was employed to analyze disturbance dynamics and their effects on herbaceous vegetation abundance at levels of both community and individual species. The PRC ordination accounted for 38% and 34% of the variation within the data sets for Tiogo and Laba, respectively. The PRC models for the first axis showed that 13% and 8% of the total variation could be attributed to time at Tiogo and Laba, respectively while treatment regime (includes the time x treatments interaction) accounted for 25% and 26% of the total variation at Tiogo and Laba, respectively. At both study sites, the first axis captured 25% to 35% of the total variation and was significant. The second axis was also significant for Tiogo but not for Laba. The PRC diagram for the first axis showed that there were two directions of departure from the control plots at Tiogo, in which fire, grazing and selective cutting treatments were not applied (Fig. 8A). The main effects of fire, selective cutting and grazing on abundance were generally positive for the herbaceous vegetation community throughout the study period; in particular, these treatments favoured species such as annual grass *Loudetia togoensis*, *Andropogon fastigiatus*, and *Andropogon pseudapricus*. The treatment interaction effects were generally negative at the community level compared to the control; this was the case throughout the study period. However there were pronounced positive effects on species such as *Andropogon gayanus*, and *Chasmopodium caudatum*. Several species had their weight close to zero, indicating that they seemed insensitive to the treatments over time. The Monte Carlo permutation tests for each sampling year revealed that the treatment regimes had significant effects on herbaceous species abundance after four (1998), and 6-10 (2000-2004) years. The PRC

diagram also showed that the extent of the fire, selective cutting, and fire \times cutting \times grazing interaction effects was greater than the effects of grazing and other interactions as evidence from the large deviation of these lines from the control (Fig. 8A). At Tiogo, two significant PRC axes were needed to summarize the large data set, suggesting that the species reacted in quantitatively different ways to the treatments.

At the second case study site, Laba, the PRC analysis for the first significant axis revealed that the treatment effects over time deviated from the control bi-directionally; the main effects of fire, grazing and selective cutting are oriented in the negative side while the interaction effects are oppositely oriented except grazing \times cutting treatment (Fig. 8B). Fire strongly influenced the abundance of herbaceous species during the study period by favouring annual grass species such as *Elionurus elegans*, *Andropogon fastigiatus*, *Diheteropogon hagerupii* and *Loudetia togoensis* while adversely affecting perennial grass species such as *Andropogon gayanus*, *Schizachyrium sanguineum*, *Andropogon ascinodis* and *Monocymbium cerasiiforme*. Grazing was the second most important factor affecting the abundance of herbaceous species over time followed by selective cutting. The extent of influence exerted by treatment interactions was generally small compared to the main effects of fire and grazing. On the basis of Monte Carlo permutation tests for each sampling year, the treatment regimes had significant effects on herbaceous species abundance after 8-12 years (2002-2006) while having marginally significant effects after five (1999) and seven (2001) years. PRC analysis has been successfully used in a variety of applications, ranging from ecotoxicological field studies (van den Brink & ter Braak, 1998; Kedwards, Maund & Chapman, 1999; Van den Brink & Ter Braak, 1999), climate change effects (Frampton, Van den Brink & Gould, 2000; Heegaard & Vandvik, 2004; Vandvik, 2004), and vegetation and disturbance dynamics (Pakeman *et al.*, 2003; Pakeman, 2004; Vandvik *et al.*, 2005; Kohler *et al.*, 2006; Britton & Fisher, 2007) to effects of ecosystem type (Neher *et al.*, 2005) and agricultural management regime (Salles, van Elsas & van Veen, 2006). In all these applications PRC appears to be a powerful tool for analyzing community responses to different perturbations over time compared with the univariate methods. The PRC method enabled us to interpret treatment effects over time not only at community level but also at individual species level. One important application of this method is to identify species that can serve as disturbance indicators. For example, Leps and Smilauer (2003) demonstrated the potential value of multivariate methods for identifying indicator species or taxa, the abundance of which may be indicative of particular environmental variables or experimental treatments. Since species with the highest weights in PRC analysis are most likely to follow the overall community response, species weight may be used for identifying potential indicator species. In our study, *Loudetia togoensis*, *Andropogon gayanus*, *Andropogon fastigiatus*, *Andropogon ascinodis*, *Chasmodium caudatum* and *Pennisetum pedicellatum* have the highest weights at Tiogo and *Andropogon gayanus*, *Andropogon fastigiatus*, *Elionurus elegans* and *Schizachyrium sanguineum* have the highest weights at Laba. Thus, they could potentially serve as indicators of fire, grazing and selective cutting disturbances in the Sudanian savanna-woodland.

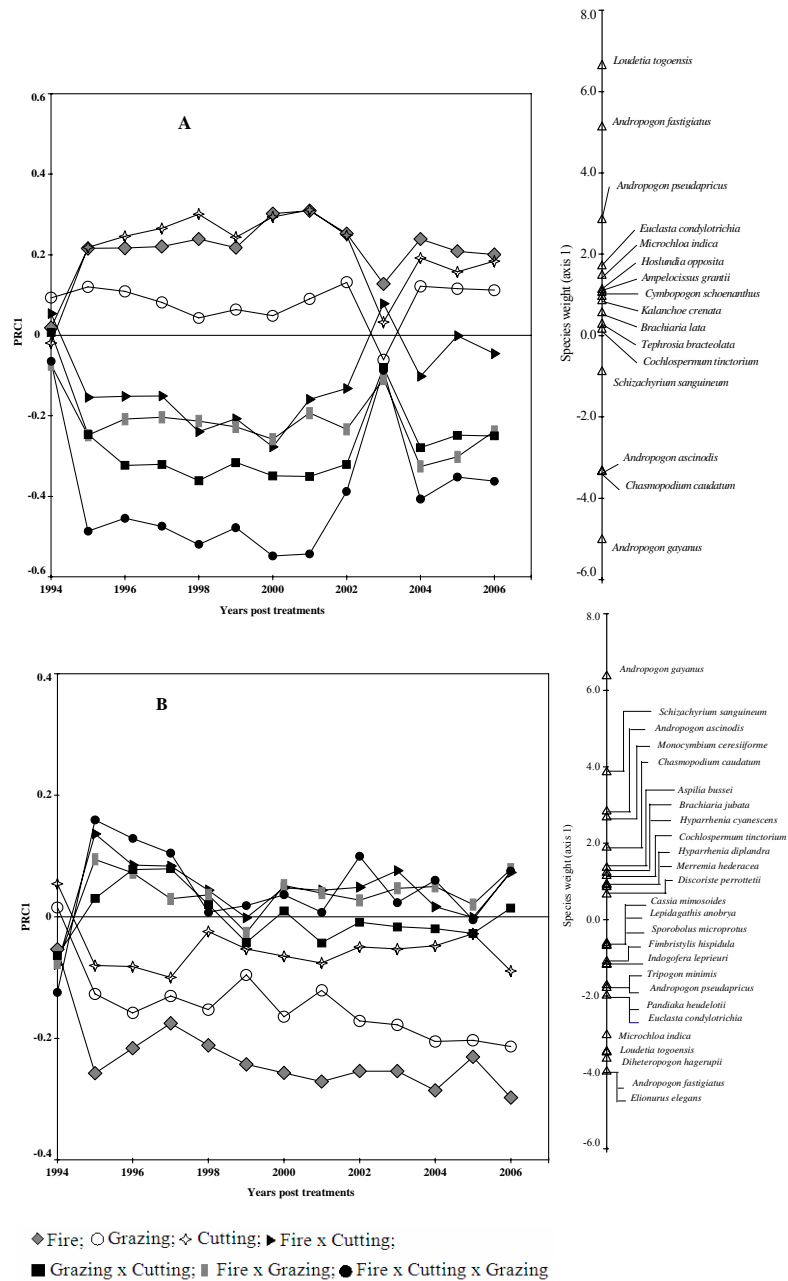


Fig. 8. Principal response curves (PRC) together with species weight diagrams representing the changes in herbaceous community response to fire, grazing, selective cutting and interactions over 13 years at Tiogo (A) and Laba (B). Species with relatively strong weight are shown for clarity.

Functional responses to disturbances

1) Soil response to disturbances

Soil physical and chemical properties of the 10 cm surface layer sampled from burnt and unburnt plots were not significantly different between treatments (Table 4). This result is in accordance with previous work (Raison, 1979; Menaut, Abbadie & Vitousek, 1992; Dembele, Masse & Yossi, 1997) that indicated no cumulative or direct effect of fire. Some long term experiments have revealed that fire does not have a noticeable effect on soil carbon (Trapnell *et al.*, 1975). An investigation of the effects of increased fire incidence conducted in the Brazilian Cerrado (Roscoe *et al.*, 2000) reports that there was no difference in C and N stocks in the top meter of soil after 21 years. Other studies however (Bird *et al.*, 2000; Parker *et al.*, 2001) support the finding that soil organic matter tends to decline in landscapes subjected to frequent burning. Data in this study does not corroborate these results and the main reason could be that the composite soil sampling procedure down to a depth of 10 cm hides the properties of the top first few centimetres. Mills and Fey (2004) compared soil from burnt and unburnt plots in a South African savanna and found that the physicochemical feedback was dramatic in the 0-1 cm layer but often not apparent in composite samples from 0-10 cm. This demonstrates the importance of the first centimetres of the soil with respect to nutrient dynamics in rangelands (Snyman, 2005). Furthermore, the fact that fire did not affect soil properties was probably due to the small increase in soil temperature at a depth of 10 cm in the burnt plots.

Table 4. Soil characteristics from samples (10 cm depth) for the different treatment combinations at Tiogo site

	Fire	No Fire
Clay (%)	26.25 ± 3.32	31.31 ± 1.85
Organic Carbon (%)	1.69 ± 0.03	1.74 ± 0.08
Fine silt (%)	15.44 ± 0.73	15.13 ± 0.94
Silt (%)	37.77 ± 1.51	33.68 ± 1.23
Sand (%)	14.38 ± 1.16	13.37 ± 1.48
Fine sand (%)	8.17 ± 0.54	6.52 ± 0.38
Total carbon (%)	0.98 ± 0.02	1.01 ± 0.05
Nitrogen (%)	0.06 ± 0.00	0.07 ± 0.00
Potassium (mg/kg)	73.93 ± 4.85	65.95 ± 5.58
Assimilated phosphorus (mg/kg)	3.00 ± 0.83	1.08 ± 0.18
Calcium (mg/kg)	901.35 ± 106.62	881.90 ± 82.98
Magnesium (mg/kg)	184.80 ± 15.72	179.20 ± 25.91
Soil pH	6.74 ± 0.11	6.60 ± 0.08
Bulk density (g/cm ³)	1.43 ± 0.01	1.41 ± 0.01

Prescribed early fire tended to decrease the steady state infiltration rate ($p = 0.073$). Although burning was repeated for eleven consecutive years, only slight differences were observed. Some studies however (Snyman, 2003) have shown a change in infiltration rate after a single accidental late fire. In the experimental early burning, fire intensities were difficult to control due to fuel load heterogeneity. The prescribed early fire is a light surface fire and only leads to

partial combustion because of high moisture content in the vegetation. The negative effects of fire on infiltration rate are likely to be the result of removal of above ground biomass and leaf litter, which increases the exposure of the soil surface to the impact of raindrops (Moyo, Frost & Campbell, 1998) that in turn leads to crusting (Mills & Fey, 2004). The mechanical energy input from raindrops increases the dispersion of clay and results in the blockage of surface pores leading to reduced infiltration in most soil types. At the experimental site, crusting could be attributed mostly to low levels of organic matter, which probably reduce aggregate stability. The steady state infiltration rate decreases significantly ($p = 0.028$) with grazing intensity (Fig. 9), indicating the importance of grazing disturbance on soil hydrology, as previously reported (Mwendera & Saleem, 1997; Rietkerk *et al.*, 2000).

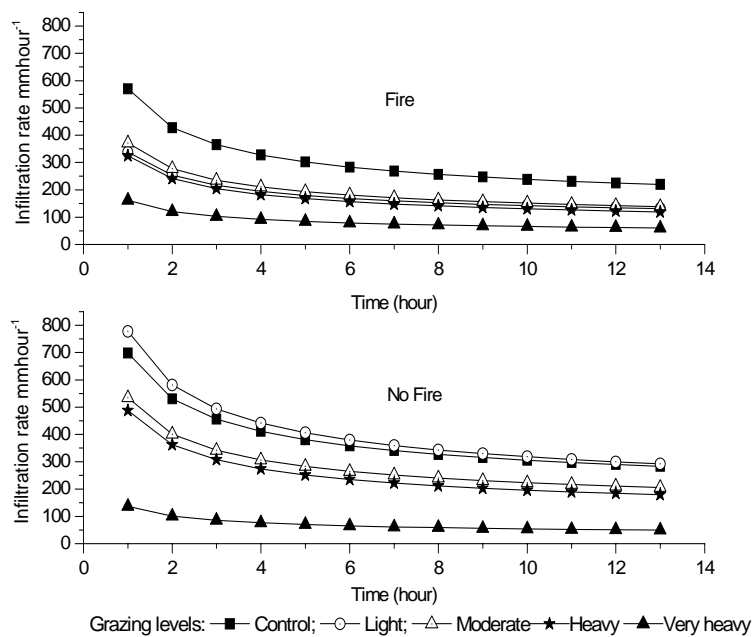


Fig. 9. Soil infiltration rate as a function of time on burnt and unburnt areas for different grazing treatment.

Grazing pressure was moderate at the study site (0.7 TLU ha^{-1}) for 10 years before this short duration grazing experiment was conducted. Livestock grazing results in mechanical pressure on the ground; trampling contributes to altered soil structure, including soil compaction and a reduction in soil porosity. The effects of soil compaction are greater when the soil is wet (Warren *et al.*, 1986). Thus, the steady state infiltration rate decreased with increased grazing pressure as a result of compaction by trampling. The high infiltration rate observed with light grazing in unburnt plots could be attributed to better decomposition of accumulated litter due to moderate trampling and change in drainage pore volume brought by disruption of aggregates, surface crust resulting from trampling. The lower

infiltration rate may be attributed to the development of soil crust under the no grazing, regime, which hindered infiltration. These results support earlier work suggesting that trampling and compaction are important in reducing soil hydrology only under high stocking rates, but that light to moderate grazing improves infiltration by reducing surface crusts (Hiernaux *et al.*, 1999).

2) Disturbance effects on aboveground phytomass

The study showed that increased grazing intensity had a tendency to reduce aboveground phytomass as a result of herbage removal and trampling. Prescribed early fire had no significant influence on the total herbaceous biomass. This was also the case for the fire and grazing interaction. At the same site, Sawadogo *et al.* (2005) found that the lack of overall effect of prescribed fire was due to disproportionate representation of annual grasses (high) and perennial grasses (low). The total biomass decreased with increasing grazing intensity, this is probably the result of increased biomass removal and the trampling pressure (static load) exerted by the animals. Heavy grazing increases soil compaction, which in turn adversely affects total productivity. McNaughton (1983) found that where plants cannot compensate sufficiently for the biomass removed by grazing, net primary productivity constantly decreases as grazing intensity increases. These results confirm that severe and repetitive defoliation occurring at high stocking rates could have lowered seasonal production. It should be noted that not only amount of rainfall but also its frequency influences plant growth (Fynn & O'Connor, 2000). Our result is consistent with a study conducted in tussock grasslands of semi-arid Australia, where above-ground biomass remained lower on burnt plots for the entire study period despite above average rainfall in all seasons except the second growing season (Bennett, Judd & Adams, 2003). It seems that not only rainfall in the first season but also during subsequent growing seasons determines post-burn productivity of herbaceous vegetation in semi-arid environments.

The effects of annual early fire on dry matter production and the cumulative effect of fire on nutrient compositions of four ecologically and socio-economically valuable grass species (*Andropogon gayanus*, *Diheteropogon amplexans*, *Chasmopodium caudatum*, and *Rottboellia exaltata*) were investigated. The results indicated that post-fire regrowth produced lower above-ground dry matter than unburned vegetation. There are three possible explanations for this. First, fire might have exacerbated water stress in this semi-arid savanna-woodland by removing standing vegetation, live or dead, thereby increasing mortality in burnt plots. Second, the recurrent fire might have exacerbated nutrient limitations in the already nutrient-poor semi-arid environment through increased nutrient losses during burning, thereby reducing plant growth. This is further evidenced by the relatively lower content of organic carbon, total carbon and nitrogen in burnt compared with unburnt plots. The loss of mineral nutrients, especially nitrogen, following frequent burning has been documented (Wan, Hui & Luo, 2001; Laclau *et al.*, 2002), and this is also reflected in the nutrient composition of above-ground biomass, notably reduced total protein content in post-burn regrowth (see below). Third, the old-growth in the unburnt plots may play an important role in sustaining growth in this semi-arid environment by ameliorating micro-climate and

maintaining reserves of plant and soil water. It is believed that standing dead vegetation and litter insulates the soil surface from excessive radiation load, thereby reducing evapotranspiration from the soil surface and the unburnt vegetation (Bennett, Judd & Adams, 2003). Overall, a combination of these phenomena would result in differences in above-ground dry matter production between burnt and unburnt plots. A marked inter-species variation in above-ground dry matter production was observed on both burnt and unburnt plots; notably the perennial grass, *A. gayanus*, was the most productive. Given the high water stress and nutrient-limitation in this semi-arid environment and given that fire exacerbates these growth limiting factors, perennial grass species have better chance of thriving in such environments than annual grass species because of their anatomical features that enable them to cope with high temperature and light intensity. Perennial grasses may resist to repeated fire due to their high level of underground reserves (Ludwig *et al.*, 2001), and their meristems being located at the base of the plant where they are protected from heat by densely packed stems and leaves (Garnier & Dajoz, 2001; Jensen, Michelsen & Gashaw, 2001). This situation could lead to biomass reduction in frequently burnt area of the two annual species *R. exaltata* and *C. caudatum* that are shade-lovers. Biomass of the dominant annual grass species *Loudetia togoensis* was strongly increased by fire (Sawadogo, Tiveau & Nygård, 2005). It could thus out-compete the other species like *R. exaltata* and *C. caudatum* in burnt areas. The significant variation in above-ground dry matter production between perennial grass species (*A. gayanus* versus *D. amplexans*) suggests the difficulty of trying to generalize about fire effects at life form level but it does highlight the fact that growth performance under resource-limited environment is rather species specific.

The chemical composition of these grass species was further investigated after several years of recurrent burning. Burning significantly reduced the amount of crude protein and neutral detergent insoluble crude protein in post-fire regrowth (Table 5). This reflects the limited soil N conditions under which the grass species were growing. Indeed, on burnt plots, soil N concentration (0.06%) was slightly lower than on unburnt plots (0.07%), and numerous studies have documented the loss of soil N due to volatilization during frequent burning (Laclau *et al.*, 2002). Fire did not, however, affect the amount of crude fat as well as cell wall and non-structural carbohydrates in post-burn regrowth. This is probably due to translocation of stored reserves between below- and above-ground biomass. Most living herbaceous biomass in the savanna is generally present below-ground (Laclau *et al.*, 2002), thus acting as a strong carbon sink. The stored carbon is then translocated during the early stage of regrowth following fire and may add-up to the photosynthetic production to such an amount equivalent to the unburned vegetation. This phenomenon of inter-organ translocation has been observed for a number of mineral nutrients in post-burn regrowth (Villegier, Schmidt & Cesar, 1979; Menaut, 1983; Laclau *et al.*, 2002). All organic compounds analyzed, however, varied significantly ($p < 0.05$) among grass species. The perennial grasses tended to have lower levels of crude protein and fat while annual grasses tended to have higher levels of non-structural carbohydrates. This could be related to their different life forms. The high concentration of fibres and lignin in perennial grasses could be related to the thick-walled bundle sheath cells in their

leaves (Laetsch, 1974). Despite this general pattern, a substantial variation in organic compounds was observed between grasses within each growth form, which is consistent with the findings by Kaboré-Zoungana (1995). The low level of total crude protein and fat in perennial grasses could also be the result of increased allocation of proteins and fats to below- than above-ground organs by perennials as an adaptive strategy to drought and other non-drought stressors in the semi-arid environment as hypothesized by several researchers (Villegier, Schmidt & Cesar, 1979; Menaut, 1983; Laclau *et al.*, 2002). These results are consistent with an earlier study in the Sudanian Zone where crude protein and fat concentration of perennial grasses were found to be significantly lower than annual grasses (Kaboré-Zoungana, 1995).

In the present study, fire did not affect the concentration of the mineral elements analyzed, with the exception of Ca, Mn and Fe (Table 5), which were significantly lower in post-fire regrowth than in unburned vegetation. Generally, burning oxidizes organically bound elements in the vegetation and litter, and these are either released in forms available to plants through ash deposition or are lost through volatilization and ash convection (Frost & Robertson, 1987). As evidenced by the soil sample analyses, fire increases the concentrations of K, P, Ca and Mg in the soil but this was not followed by concomitant increases in post-fire regrowth. The extent to which the addition of nutrients via ash contributes to enhanced soil nutrient supply and consequently vegetation nutrient status depends on the total amount of available nutrient in the soil. It seems that the amount of nutrients released via ash is not large enough in our burnt plots to substantially increase the total amount of plant available nutrients; this is consistent with the results reported by Van de Vijver *et al.* (1999) for an East African savanna. It is likely that the reduced concentrations of some mineral elements (Ca, Mn and Fe) in post-burn regrowth might be related to their low mobility within plant tissues and to foliar leaching. The concentrations of mineral elements also varied significantly between grass species; notably those of P, Mg, K, Ca, Zn, Cu, Mn and Mb. This could be related to the nutritional requirements and uptake efficiency of each particular species, as documented in an earlier study (Kaboré-Zoungana, 1995). Interestingly, all grass species, irrespective of the fire treatment, have higher concentrations of most mineral elements than required for livestock production in tropical grassland ecosystems (Payne & Wilson, 1999). Thus they appear to be suitable for animal nutrition, although deficient in Ca, P, Na and Mb. This finding is consistent with other studies from tropical grasslands (Jumba *et al.*, 1995). Knowledge of the energy content of a particular food is helpful for feeding animals according to their nutrient requirements and to support a desirable level of production (Mlay *et al.*, 2006). Fire did not affect the estimated net energy and digestibility of the studied grass species. This could be explained by the fact that burning did not significantly affect cell wall constituents which are known to decrease digestibility (Mlay *et al.*, 2006). However, the net energy for lactation, the relative feed value and relative forage quality were significantly higher for annual than perennial grasses. This is related to the fact that they have higher concentrations of proteins, fats, starch and sugars than the perennial grasses.

Table 5. Summary of selected chemical nutrients affected by cumulative burning

	<i>Andropogon gayanus</i>	<i>Diheteropogon amplectens</i>	<i>Chasmodonium caudatum</i>	<i>Rottboellia exaltata</i>	Main effect (fire)
CP%	Fire	3.35 ± 0.35	4.45 ± 0.05	5.30 ± 0.40	4.11 ± 0.33*
	No Fire	3.30 ± 0.00	5.40 ± 0.30	6.25 ± 0.25	4.63 ± 0.47
	Main effect (Species)	3.33 ± 0.14a	4.93 ± 0.30b	5.78 ± 0.34c	
NDICP%	Fire	1.55 ± 0.25	1.65 ± 0.05	1.95 ± 0.05	1.74 ± 0.09*
	No Fire	1.55 ± 0.05	1.95 ± 0.05	2.75 ± 0.05	2.05 ± 0.17
	Main effect (Species)	1.55 ± 0.10a	1.80 ± 0.09a	2.35 ± 0.23b	
Ca%	Fire	0.19 ± 0.01	0.18 ± 0.01	0.24 ± 0.02	0.25 ± 0.04*
	No Fire	0.20 ± 0.01	0.23 ± 0.02	0.31 ± 0.03	0.31 ± 0.05
	Main effect (Species)	0.19 ± 0.01a	0.20 ± 0.02a	0.27 ± 0.03b	
Fe ppm	Fire	137.00 ± 4.00	177.00 ± 22.00	325.00 ± 68.00	206.00 ± 30.09*
	No Fire	203.00 ± 47.00	250.00 ± 48.00	257.00 ± 47.00	274.75 ± 31.22
	Main effect (Species)	170.00 ± 27.10a	213.5 ± 30.14a	291.00 ± 39.04a	287.00 ± 60.92a
Mn ppm	Fire	82.50 ± 1.50	124.50 ± 6.50	61.00 ± 5.00	75.25 ± 12.73*
	No Fire	91.50 ± 2.50	157.00 ± 4.00	65.00 ± 3.00	88.50 ± 16.47
	Main effect (Species)	87.00 ± 2.86a	140.75 ± 9.89b	63.00 ± 2.65c	36.75 ± 2.53d

CP: Crude Protein; NDICP: Neutral Detergent Insoluble Crude Protein.

* Significant overall main effect, $p < 0.05$. For species, means with different letters are significantly different based on Tukey's HSD test.

Implications to equilibrium and non-equilibrium paradigms

There exist two opposing views on disturbance dynamics in savanna ecosystems: the equilibrium and non-equilibrium paradigms (Tainton, Morris & Hardy, 1996). According to the equilibrium theory, once disturbance has occurred in a system, the system state either returns to its former equilibrium state or equilibrates to a new domain of attraction. Here, disturbance is considered as the main factor influencing the vegetation dynamics. On the contrary, many savanna ecosystems, particularly in arid and semi-arid environments, follow non-equilibrium dynamics in that a steady state is never achieved. In these systems, abiotic factors (notably rainfall distribution, amount and intensity) seem to have an overriding influence on vegetation dynamics than do disturbance agents per se. Dynamics in disequilibrium systems are characterized by periods of rapid change resulting from the coincidence of various factors (e.g. intense grazing following a drought) followed by periods when the system is relatively insensitive to manipulation. Generally it is believed that the equilibrium theory seems fit to a system where rainfall is relatively consistent and predictable and where the vegetation community is comprised of largely of perennial plants (Illius & Hodgson, 1996). The non-equilibrium dynamics best suits a system where rainfall is unpredictable and where the annual components of the vegetation community is large. It seems that the Sudanian savanna-woodland, where the thesis work has been conducted, follows the non-equilibrium dynamics as evidenced from the highly significant inter-annual variation in herbaceous flora while the effects of fire, grazing and selective cutting were limited and minimal. Generally, non-equilibrium systems are unpredictable in their response to management, but opportunities to manipulate the system in a certain direction may occur under a particular set of conditions. For example, moderate levels of grazing could be adopted as management tool to reduce the availability of fuel loads during years of high phytomass production, thereby reducing the risk of severe late fire. Prescribed early fire is essential to remove accumulated low-quality residual material, to induce a uniformly palatable flush of new growth and prevent catastrophic late fire provided that the timing of burning, and weather condition are judiciously selected. Selective cutting of trees can be done taking into account the spatial distribution of the woody components as they may create patchiness in the vegetation.

Conclusions and Recommendations

The effects of disturbance on the structure and functions of the savanna-woodland ecosystem were evaluated with emphasis on herbaceous component. Characterization of fire behaviour in relation to grazing disturbance indicated that moderate levels of grazing can be used as a tool to control fire behaviour in the savanna-woodlands. Early fire could therefore be adopted as a valuable option for minimizing the effect of late accidental fire. Livestock reduces herbaceous biomass thus decreasing fire severity by lowering fire temperature and lethal temperature residence time. The dominant grass type during prescribed burning

influenced the moisture content of the fuel, which in turn reduces the fire temperature. Wind direction affected fire temperature and residence time, flame height and rate of spread suggesting that managers should consider back fire to control fire propagation and intensity. The empirical fire behaviour model is reasonably good, and could serve as a tool to guide prescribed burning in the study area.

The long-term multi-factor study on herbaceous vegetation responses to several disturbance regimes provides evidence that the species composition, diversity and abundance in Sudanian savanna-woodlands exhibit significant inter-annual variability that balances the main or interaction effects of grazing, fire and selective tree cutting. This substantial inter-annual variation in vegetation attributes is related to several stochastic factors such as rainfall, stocking rate, grazing intensity, competition. The responses of the herbaceous flora to disturbances, particularly fire and grazing, were site-specific, suggesting the importance of landscape-scale approaches to understand the impact of disturbances on the composition, structure and diversity of savanna-woodland ecosystems. Provided that wet season grazing is kept at moderate intensity, the management of savanna-woodlands could be integrated with livestock husbandry, as it is one of the main sources of livelihood and revenue for the local people in Burkina Faso. The current level of selective cutting (50% of the merchantable standing volume) seems to have no effect on herbaceous vegetation; further research may be needed to evaluate other cutting intensity that may bring the expected beneficial effects of canopy removal. The Principal Response Curves analysis of disturbance dynamics in the savanna-woodland offers a great opportunity to resource managers, since it allows identification of potential indicator taxa that could be used for monitoring effects of disturbance regimes on the herbaceous component of the savanna-woodland.

With regard to functional responses, prescribed early fire did not significantly affect the steady state infiltration rate. Therefore, early fire seems to be a good management option to compromise between total fire protection (which is utopian) and the occurrence of very intense late fire that is inevitable in the study area if early fire is not applied. Heavy grazing during the wet season, however, significantly reduced the steady state infiltration rate and above ground phytomass in the studied ecosystem. From savanna-woodland management point of view, grazing intensity in the forest during the rainy season should not ideally exceed a moderate level so as to prevent the deleterious impact of herbivores on soil and vegetation. Annual fire reduces the above-ground biomass of post-fire regrowth of the studied species. The fire effect on chemical composition of post-fire regrowth was not, however, substantial compared with unburnt vegetation. Although annual early fire resulted in lower above-ground dry mass in some grass species, its effect is still comparably less to the most severe late fire we often observe. Thus, the application of annual early fire as a tool for multiple use management of savanna-woodland could continue with due cautions to the timing of burning, weather conditions and other possible factors that influence fire intensity.

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Résumé en Français (French summary)

Le pâturage, le feu et la coupe sélective de bois sont les perturbations majeures qui modèlent la diversité biologique et la productivité des écosystèmes savaniques. Cependant, leurs impacts sont très variés et peu compris. La présente étude a concerné les réponses structurelles et fonctionnelles de la savane arborée soudanienne à ces perturbations avec un accent particulier sur la strate herbacée.

Le combustible et le comportement du feu ont été caractérisés en relation avec le pâturage, la forme biologique des graminées dominantes ainsi que la direction du vent. Les résultats ont montré que le pâturage modéré a réduit significativement la phytomasse consommée par le feu. Le feu brûlant dans la direction du vent progressait plus vite et les flammes étaient moins hautes que celui brûlant dans le sens opposé. La température moyenne maximale du feu était plus élevée en zone non pâturée, dans les végétations à dominance de graminées annuelles, dans les parcelles brûlant dans le sens de la direction du vent ainsi qu'à la surface du sol. La durée de la température létale pour les tissus végétaux (>60°C) a évolué dans le même sens que la température du feu. L'examen des réponses structurelles des herbacées a montré que le pâturage a augmenté l'abondance et la diversité spécifique des graminées pérennes. Le feu a augmenté la richesse spécifique des graminées annuelles. La coupe sélective de bois n'a eu d'effet significatif sur aucun des paramètres de la végétation. L'effet combiné du pâturage, du feu et de la coupe sélective a augmenté la diversité des phorbes. Les réponses structurelles de la végétation ont montré une variation temporelle significative pouvant s'expliquer en partie par les variations interannuelles de la pluviosité, de la charge animale et de l'intensité du feu. L'analyse multivariée dénommée « Principal Response Curves » a prouvé que les effets de ces derniers dépendaient des espèces. Les réponses fonctionnelles de l'écosystème aux perturbations ont été caractérisées à travers l'impact de celles-ci sur les caractéristiques physico-chimiques et les propriétés hydrologiques du sol, sur la biomasse épigée et la teneur en éléments chimiques des herbacées. Le pâturage intensif a eu pour effet de réduire la capacité d'infiltration en eau du sol ainsi que la biomasse herbacée épigée par une accentuation du piétinement et de la consommation d'herbe. Le feu précoce annuel a eu une tendance à réduire la vitesse d'infiltration de l'eau du sol notamment à travers son effet sur la matière organique du sol; la vitesse d'infiltration est expliquée par 34% de la matière organique. Il n'y a pas eu d'effet à long terme du feu précoce annuel sur les propriétés physico-chimiques du sol et la biomasse herbacée épigée totale. D'autres études de l'effet du feu sur la production de biomasse et sur la composition chimique de quatre graminées ont montré une réduction significative de la matière sèche épigée, des teneurs en protéines brutes, Ca, Fe et Mg.

En conclusion le pâturage modéré pourrait servir à modifier le comportement du feu, pour réduire la susceptibilité du sol à l'érosion et pour maintenir une biomasse herbacée appréciable. Etant moins intense, le feu brûlant dans le sens contraire du vent est recommandé pour l'aménagement multi-usages des forêts soudanaises. La variation des réponses structurelles de la végétation en fonction du site souligne l'importance des approches paysagères pour mieux comprendre les impacts des perturbations sur les écosystèmes savaniques soudanais.

Mots clés: Feu; pâturage; coupe sélective de bois; production de biomasse; diversité herbacée; infiltration du sol; composition chimique; Burkina Faso; Afrique de l'Ouest.